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OBSERVATIONS ON THE PERENNIAL CANKER FUNGUS

GLOEOSPORIUM PERENNANS ZELLER & CHILDS

By E. H. WILKINSON, *Research Station, Long Ashton, Bristol*

(With Plate II and 3 Text-figures)

1. Introductory

A preliminary note (Wilkinson, 1943) recorded that a fungus frequently isolated from dieback and canker lesions of apple shoots and from storage rots of apple fruits in England was identical with *Gloeosporium perennans* Zeller & Childs, described in the U.S.A. as the cause of the apple disease known as Perennial Canker. That identification is confirmed here and further details are given of the isolation, cultural characteristics and pathogenicity of the fungus, in comparison with the American findings.

The disease caused by *G. perennans* in the U.S.A. was termed Perennial Canker because the lesions produced could increase in size for a period of six or seven years with the production of successive concentric rings of callus. Subsequent work (Childs, 1929; Cooley & Shear, 1931; Brown, 1932; McLarty, 1933) has shown that annual extensions of the canker do not occur in the U.S.A. unless the limiting callus layer is injured by low temperatures or Woolly Aphis attack. In England it has been shown (Wilkinson, 1944) that the most serious phase of the attack by *G. perennans* is the dieback of summer-pruned trees, and that the cankers formed are normally of the restricted type with a single callus layer. Exceptionally, two rings of callus are formed, following Woolly Aphis injury. Further work on the conditions determining extension of the cankers is described here.

Cross-inoculations show that *G. perennans* isolated from shoots causes a rot of apple fruits in this country. This apple rot is not distinguishable by superficial examination from that caused by *G. album* and it was suggested (Wilkinson, 1944) that the disease in the field should be included under the term Bitter Rot. Comparisons are made below of the lesions caused on apples by *G. album*, *G. fructigenum* and *G. perennans*.

2. Identity and cultural characteristics of the pathogen

Zeller and Childs named the fungus causing Perennial Canker *Gloeosporium perennans*, having 'conidia hyaline, irregular in shape and size, mostly ellipsoidal, usually larger at one end, seldom slightly curved, 12–20 × 4–6 μ; producing secondary conidia in culture; secondary conidia hyaline, variable in size, 3–10 × 1–2 μ, ovoid to ellipsoid, sometimes curved'.

Vol. XXVIII, Parts I & II: issued 4 June 1945

A description of Perennial Canker as it occurs in England and the pomological aspect of the attack have been given in a previous publication (Wilkinson, 1944).

Sporing material of the fungus, isolated by the author from infected branches and fruits in this country, was obtained by incubating infected branches and apples in moist chambers at 21° C. for three days. Spore suspensions from the two sources were made and plated out on 2 % malt-extract agar from which monoconidial isolations were obtained. The isolations, whether from cankers or apple rots, collected from various parts of the country, were similar. Initially, a small tuft of white mycelium is formed which grows slowly, the thallus being little more than 1 in. in diameter after twenty-three days. At first the mycelium turns grey, then a delicate pink, but eventually becomes dirty white and assumes a ragged woolly appearance. In plate cultures, the marginal growth is submerged; no cracking of the agar occurs, but a brown discoloration is evident when the cultures are a few days old. In tube cultures the fungus produces black apothecium-like bodies on the underside of the agar slope; they are compressed against the glass wall of the culture tube and cause the lifting of the agar cylinder. No unmistakable asci or ascospores have been observed. Similar incipient apothecia were described by Kienholz (1939) who also reported the discovery of the perfect, apothecial, stage of *G. perennans* occurring naturally on apple tree cankers; this he named *Neofabraea perennans*.

Acervuli appear slowly when a single isolation is grown on plate cultures, but their formation is appreciably accelerated when eight to ten colonies are grown on the same plate. They are formed irregularly on the agar surface, arising mainly from the submerged marginal mycelium or over the surface of the aerial mycelium. The former arise as small masses of compact, dark, undifferentiated hyphae, the sporing layer being distinctly concave, whereas those formed on the surface of the thallus are frequently found at the distal end of comparatively long necks of sterile, hyaline hyphae.

The conidiophores are erect, branched, hyaline, septate, approximately three to four times as long as the spores, the latter being budded off terminally and successively, and accumulating as small white masses when young, but tending to become pale yellow with age. The conidia are non-septate, hyaline, irregular in size, straight, usually larger at one end and mainly ellipsoidal measuring 10·5–18·7 × 3–6 μ (Text-fig. 1 *b*).

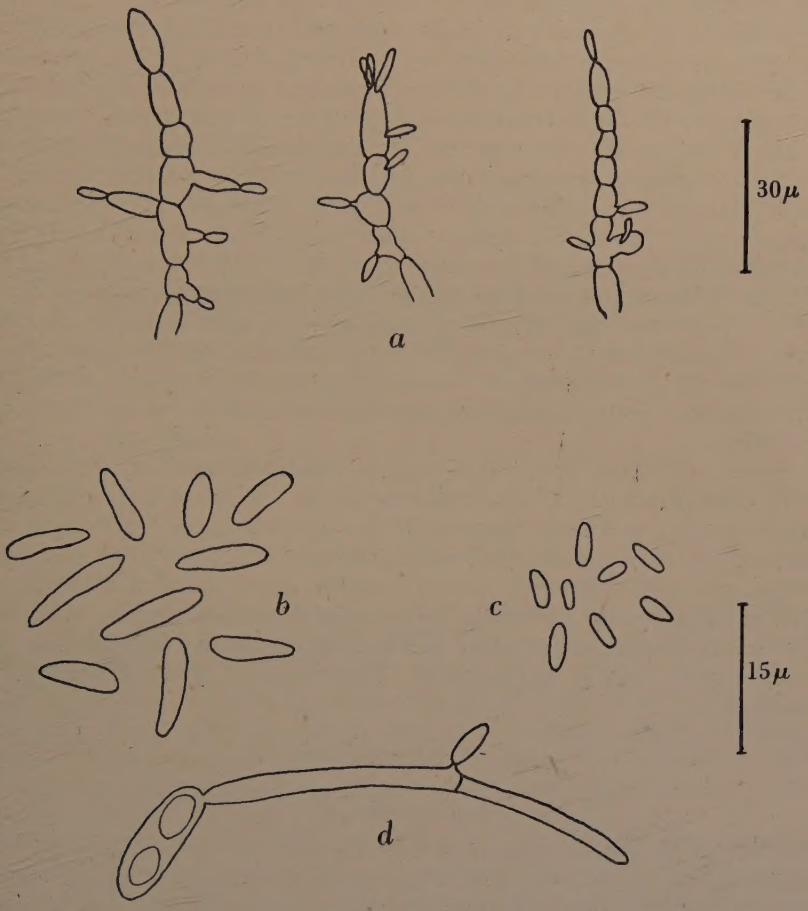
Conidia produced on 2 % malt-extract agar by isolations of the fungus from apple fruits and branch infections measured 4·5–21 × 1·5–6 μ. This range is greater than that given by Zeller and Childs as secondary conidia, which were readily produced in culture, are included.

Formation of secondary conidia

G. perennans forms secondary conidia in culture and aqueous nutrient solutions, a fact reported by Zeller and Childs (1925), but in addition I have observed them on natural lenticel rots and branch infections. Using spores taken from a culture of the fungus isolated from a lenticel

rot of Laxton's Superb, their formation at laboratory temperatures was followed in hanging drops of sterile distilled water and 0·1 % sucrose solution and also on 2 % malt-extract agar.

In the hanging drops, germination occurred readily after five hours, the germ-tubes originating at the ends of the spores, a central septum being formed when two developed from the same spore. Very occasionally a



Text-fig. 1. Formation of secondary conidia in *G. perennans*. (*a*) On 2 % malt-extract agar. (*b*) Normal conidia from Bitter Rot lesion. (*c*) Secondary conidia formed in 0.1 % sucrose solution. (*d*) Budding-off of secondary conidium in 0.1 % sucrose solution.

germ-tube is produced on the side close to the septum. In sterile distilled water secondary conidia were formed after seventy hours, and in 0·1 % sucrose solution after forty-seven hours. Each secondary conidium is produced independently, but successively, from a point immediately below each septum of the germ-tubes and when liberated floats away, when the formation of another begins (Text-fig. 1 *d*). In both solutions they are small, hyaline, non-septate, ellipsoidal (Text-fig. 1 *c*) measuring 3·0–6·0

× 1·5 μ (mean 5·0 × 1·5 μ) in sterile distilled water, and 3·0–9·0 × 1·5–3·0 μ (mean 5·9 × 1·87 μ) in 0·1 % sucrose solution. The secondary conidia failed to germinate in either solution over a period of five days. Zeller and Childs (1925) give measurements of 3–6 × 1–1·5 μ.

On 2 % malt-extract agar the spores germinated readily in a manner similar to that observed in aqueous solutions. At an early stage the germ-tubes became closely septate and formed numerous branches. After forty-seven hours secondary conidia were produced in large numbers at the apex, and from points immediately below the septa, of the germ-tubes, later becoming detached and adhering in masses around the hyphal growth (Text-fig. 1 *a*). They measured 6·0–9·0 × 1·5–2·25 μ (mean 7·6 × 2·0 μ). As the colony increased in size so also did the size of the conidia liberated; in fact after seventy hours normal conidia were being budded off which in their turn germinated and had produced a further crop of secondary spores after 120 hours. Secondary spores were never seen to germinate. Some spores having one or two septa were also observed which may have originated from fragmentation of the mycelial growth. Hence when a spore of *G. perennans* germinates on malt-extract agar a small amount of hyphal growth becomes surrounded by large numbers of secondary and normal conidia after five days. Eventually the hyphae grow out radially and no further spore formation on these extensions is observed after seven days.

The fungus isolated by me thus agrees closely with the original description of Zeller and Childs. The range in size of the normal spores is about the same as that given by them, while the formation of secondary conidia in nutrient solutions is identical with that described by Zeller and Childs and the size range corresponds very closely. Black apothecial-like bodies in culture described by Kienholz (1939) were also observed in my isolations.

My isolation matches none of the British species of *Gloeosporium* listed (Grove, 1937), but it agrees with Zeller and Child's description of *G. perennans*.

3. Pathogenicity

Cross inoculations

(*a*) *Bitter Rot fungus into branches.* A fourteen-day-old isolation of *G. perennans* from a lenticel rot of Allington Pippin and trees of the varieties Bramley's Seedling, Cox's Orange Pippin, Laxton's Superb and Worcester Pearmain were used for these experiments. On 9 May 1941, four inoculations were made on each variety by cutting a side branch flush with its stouter member and placing a square of inoculum with the mycelium in contact with the cut surface, the operation being completed by binding the wounds with a crêpe-rubber bandage. These were removed one month later when eleven out of sixteen inoculations were showing a marked swelling, accompanied by the splitting and peeling of the bark, 1 in. above and below the point of inoculation. These symptoms became more pronounced, and after ten weeks, distinct cankers had been formed from all sixteen inoculations. They varied from small, black, flattened lesions

on Bramley's Seedling (Pl. II, fig. 1) to those on Cox's Orange Pippin which were 3–4 in. long, showing extensive peeling of the bark, and completely girdling the branches.

In July the bark over each canker became raised at many points producing a blistered appearance. Each swelling finally burst to expose numerous, grey coloured acervuli which had originated sub-epidermally on the cortical tissues. Under humid conditions they liberated small white masses of spores, and re-isolation from these gave pure cultures of *G. perennans*. During the autumn of the same year canker development was arrested by the formation of a callus barrier which isolated completely the diseased from the healthy tissues. Examination in the autumns of 1942 and 1943 showed no further extension beyond this barrier.

A similar series of inoculations was made on 11 November 1941. Cankers 2–3 in. in length were formed by the end of the year when development slowed down presumably as the result of lower temperatures, no callus barrier being formed. The cankers developed slightly toward the end of March 1942, but by April the twelve cankers on three apple varieties had become completely callused off. The lesions on Laxton's Superb continued to expand until midsummer when they, in their turn, were isolated from healthy tissues by callus barriers. Exposed acervuli, liberating small white masses of spores were observed on most of the cankers in May 1942.

Inoculations on uninjured bark of three-year-old branches of the above four apple varieties were made on 9 May and 11 November, but no cankers were formed.

The cankers which developed as the result of inoculations carried out on 11 November 1941, were used in the following experiment in September 1942: Two of the four cankers on each variety were slightly injured by scraping the callus layer with a sterile needle, the remaining two being left uninjured. All cankers were bound with crêpe-rubber bandages which were removed one month later. Extensions of the original lesions developed on six out of the eight wounded cankers—those on Bramley's Seedling failing to show any additional increase—to the extent of 1 in. but these in their turn were callused off by April 1943. Those cankers left unwounded failed to show any further enlargement.

(*b*) *Perennial Canker fungus into apples.* Apples of the variety Allington Pippin were surface-sterilized and inoculated with mycelium from a ten-day-old culture of *G. perennans* isolated from a canker of Early Victoria and retained in moist chambers at laboratory temperatures. Rotting proceeded in a radial manner, forming circular sunken lesions mostly having a dark brown marginal zone surrounding a central pale brown area. The rate of spread was slow, one rot being 1½ in. in diameter after thirty-seven days. Sporing bodies, originating subepidermally, appeared after twenty-five days as small blisters on the surface of the rots, finally rupturing the skin to become exposed as grey acervuli liberating small white masses of spores. Re-isolation from both spores and rotted tissues yielded pure cultures of *G. perennans*.

Similar rots were produced when apples were inoculated with *G. perennans*

isolated from dieback lesions of Cox's Orange Pippin and Laxton's Superb.

To investigate whether *G. perennans* from branch infections would infect apples through lenticels or uninjured skin the following experiment was performed. A Bramley's Seedling fruit was surface sterilized and ten small glass tubes were attached perpendicularly to its surface with medicinal vaseline so that a single lenticel was enclosed by the attached end of each tube. A second fruit was treated similarly, but the tubes were placed over unbroken skin with no lenticels present. A small volume of a conidial suspension from a culture of *G. perennans*, isolated from a canker of Early Victoria, was pipetted into each tube so that no air lock was formed between the suspension and the apple skin. The tubes were then sealed with cotton wool plugs. After five days the tubes were removed and the apples kept under observation. The fruit with the inoculated lenticels developed ten small circular lesions each producing numbers of sporing bodies from which the fungus was re-isolated in a pure state (Pl. II, fig. 2). The fruit inoculated on the unbroken skin failed to produce any rots.

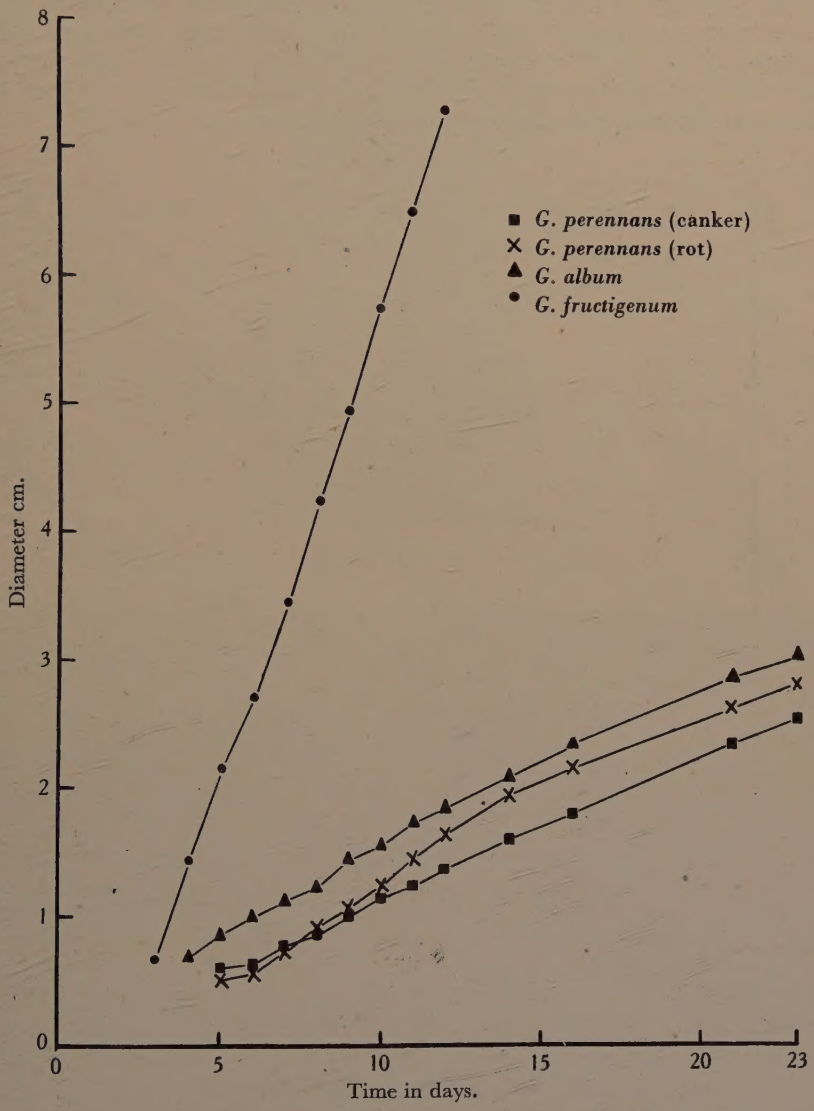
4. Comparison of fungi causing Bitter Rot of apples

Bull's Eye Rot (Fisher, 1925) and Delicious Spots (Brien, 1932) are names given to the fruit rot caused by *G. perennans* in the U.S.A. and New Zealand respectively. In England, however, this apple rot is not distinguishable by superficial examination from Bitter Rot caused by *G. album* Osterw. It was suggested (Wilkinson, 1944) therefore that it should also be included under the name Bitter Rot, thus adding a third species of *Gloeosporium* to the two already known to cause this disease.

Apples inoculated with *G. album* and *G. perennans* produce rots typically having a pale brown or yellow centre surrounded by a darker brown marginal zone with a lenticel usually situated in the middle of each rot. The rate of development of the lesions is nearly identical and sporing bodies appear after twenty to twenty-five days. The acervuli of both fungi burst through the skin to become exposed as small grey bodies which, under moist conditions, liberate white masses of spores embedded in mucilage. In both types of rots, spores have been observed issuing from the acervuli as thin white tendrils. The acervuli are more frequently scattered irregularly over the surface of the rots but are occasionally arranged concentrically especially on those caused by *G. album*.

Separation of the two pathogens by these visual symptoms is not possible and can only be made by examination of the spores which are quite distinct. Those of *G. album* are hyaline, non-septate but distinctly curved, measuring $12–27 \times 4–5\,\mu$, whereas those of *G. perennans* are hyaline, non-septate and mainly ellipsoidal, measuring $4{\cdot}5–18 \times 2{\cdot}2–6\,\mu$. In contrast, the rot caused by *G. fructigenum* is readily distinguished by the more rapid rotting, the lesions being darker and characterized by the production of greyish black surface mycelium and glutinous masses of spores which are ochraceous-buff to *o*-orange (Ridgway, 1912). In addition, inoculations

made by me indicate that *G. album* and *G. fructigenum* are both non-parasitic, whereas *G. perennans* is an active wound parasite, on apple branches.

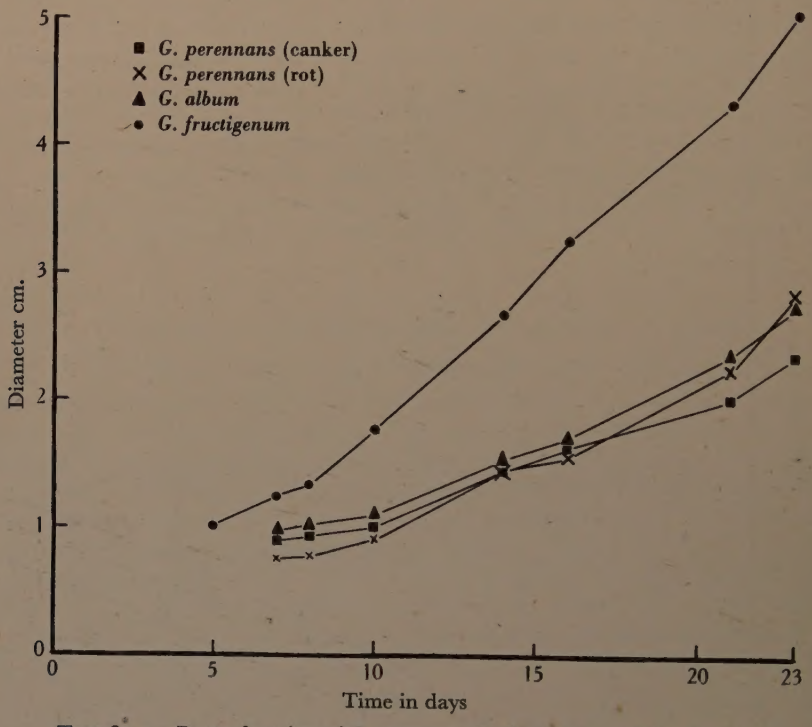


Text-fig. 2. Growth rate of *G. perennans*, *G. fructigenum* and *G. album* on 2% malt-extract agar at 22° C.

The rate of growth in culture of *G. perennans* from branch and fruit lesions and the rate of decay it causes in the fruit were compared with those of *G. album* and *G. fructigenum* under identical conditions using monoconidial isolations.

(*a*) *In culture*

Pieces of inoculum 0·2 cm.sq. were cut from the margins of fourteen-day-old cultures of the four isolations and placed in the centre of 2 % malt-extract agar plates. Eight plates were inoculated with each fungus and kept at 22° C. The diameter of the mycelial growth was measured daily over a period of twenty-three days. The results are given in Text-fig. 2 each point representing the mean of eight diameters.



Text-fig. 3. Rate of rotting of *G. perennans*, *G. fructigenum* and *G. album* in Bramley's Seedling at 22° C.

(*b*) *In apples*

Sixteen fruits of the variety Bramley's Seedling were immersed in 1/1000 $HgCl_2$ solution for five minutes, washed in running water for ten minutes, dipped in absolute alcohol, and flamed. Each fungus was inoculated into four apples in two places by bringing back a flap of skin and inserting a piece of inoculum 0·2 cm.sq. taken from fourteen-day-old cultures. The skin flaps were replaced and sealed in position by a thin layer of medicinal vaseline, the apples being placed in moist chambers at 22° C. and daily measurements of the diameters of the rots taken over a period of twenty-three days (see Text-fig. 3), each point again representing the mean of eight diameters.

Fig. 1

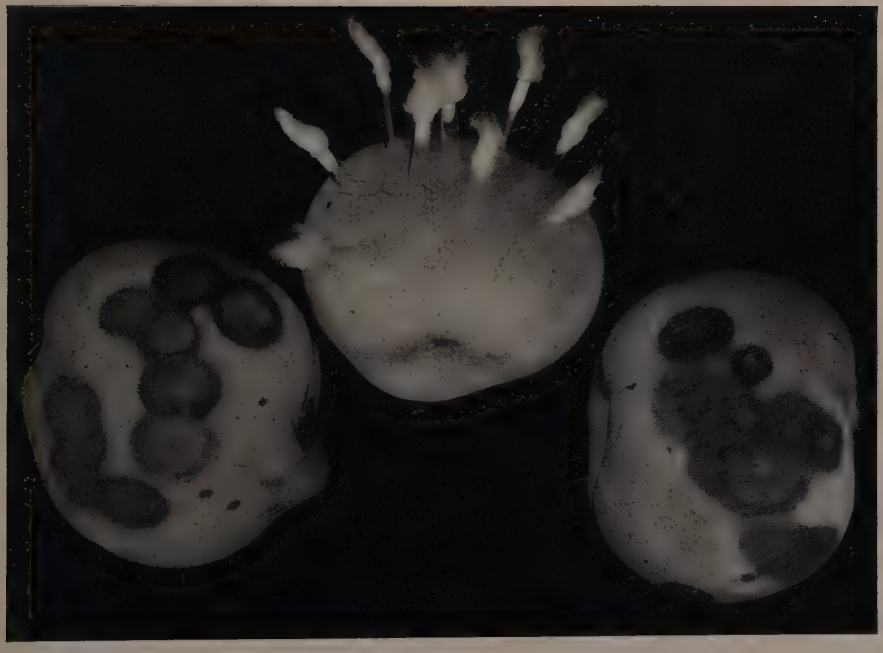


Fig. 2

5. Summary

1. A fungus isolated from canker and dieback of branches and apple rots in this country is shown to be *Gloeosporium perennans* Zeller & Childs.

2. Cross inoculations demonstrated the identity of the fungus causing branch lesions with that infecting fruits.

3. Some morphological characteristics of *G. perennans* are described.

4. Controlled infection experiments, show that *G. perennans* is an active wound parasite of apple branches, but is unable to penetrate uninjured bark; it cannot penetrate the unbroken skin of the fruit but can traverse the skin through a lenticel.

5. The rate of growth of the fungus and the rate of decay it causes in apple fruits are compared with those of *G. album* and *G. fructigenum*. *G. perennans* grows at approximately the same rate as *G. album* and much more slowly than *G. fructigenum*.

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EXPLANATION OF PLATE II

Fig. 1. Perennial Canker on Bramley's Seedling.

Fig. 2. Lenticel infection by spore suspension.
Left: *G. perennans*. Right: *Nectria galligena*. Centre: Technique used.

(*Accepted for publication* 11 *January* 1945)

STUDIES ON SOME DISEASES OF SAINFOIN (*ONOBRYCHIS SATIVA*)

I. RING-SPOT CAUSED BY *PLEOSPORA HERBARUM* (PERS.) RABENH.

By S. J. HUGHES, *University College, Cardiff*

(With Plate III and 3 Text-figures)

It appears from the literature that the diseases of sainfoin, or French grass as it is called in Glamorgan, have received very little attention in the past. Oudemans (1921) records seventeen different species and varieties of fungi as having been found on sainfoin in Europe and most of them are known only from the original diagnoses. Only three of these appear to have been recorded as causing diseases of sainfoin in Britain; the diseases are, Leaf Spot, caused by a fungus referred to *Ascochyta Orobi* Sacc.; Rust, *Uromyces Onobrychidis* (Desm.) Lév., and Mildew, *Erysiphe Polygoni* DC. (pro parte ≡ *E. Martii* Lév.).

Two diseases found in this country and caused by fungi not mentioned in Oudemans' list are: Chocolate Spot caused by *Botrytis cinerea* Fr. which has been observed in Glamorgan to kill flower buds and cause a stem rot under very moist conditions; and Rot caused by *Sclerotinia Trifoliorum* Erikss., first recorded on sainfoin in this country by Carruthers (1898), and reported several times since, by Carruthers (1902, 1907), Biffen (1910, 1912, 1913, 1918, 1920) and more recently by Rees (1936) and Moore (1944).

Grove (1935) found *Placosphaeria Onobrychidis* Sacc. (? ≡ *Diachora Onobrychidis* Müll. teste Grove) on *Lathyrus* at Kew, and not on sainfoin, the first recorded host for this fungus. Massee (1915) described by a brief translation of the account of Prillieux and Delacroix (1893) a leaf spot of sainfoin caused by *Ramularia Onobrychidis* Prill. & Delacr. This, however, is a doubtful British record and the fungus is not included in the List of Hyphomycetes recorded for Britain (Wakefield & Bisby, 1941). I found *R. Onobrychidis* on sainfoin in December, 1943.

This paper is the first of a series on diseases of sainfoin in Britain, particularly in Glamorgan. Sainfoin once played 'an important part in the agriculture of the Vale of Glamorgan especially on the thinner and drier Lias soils . . .' (Rees, 1936), and at one time it was grown on the Gower Peninsula. In 1944, the sainfoin growing area in this county comprised some seventy acres, at Gileston, Llantwit-Major and Southerndown, in the Vale of Glamorgan. It is also grown to a small extent in South Monmouthshire.

1. Ring-Spot, caused by *Pleospora herbarum* (Pers.) Rabenh. (Stat. conid., *Stemphylium botryosum* Wallroth).

This leaf Ring-Spot disease has not, as far as is known, hitherto been recorded in Britain; it was first found at Llantwit-Major and at the Cardiff University College Agricultural Experimental Plot at Ely in May 1943.

Frequent surveys have now shown that it is always present on sainfoin grown in Glamorgan. Ring-Spot, whilst present all the year round, is found in greatest abundance in the spring; it was very common at all stations in April 1944.

The ring-spot (Pl. III) typically shows a circular light brown area with a darker and well-defined margin. Young lesions are entirely dark brown but the central zone becomes lighter as the infection spreads. Under favourable conditions of moisture the fungus produces conidia abundantly, giving the spot a very conspicuous sooty appearance.

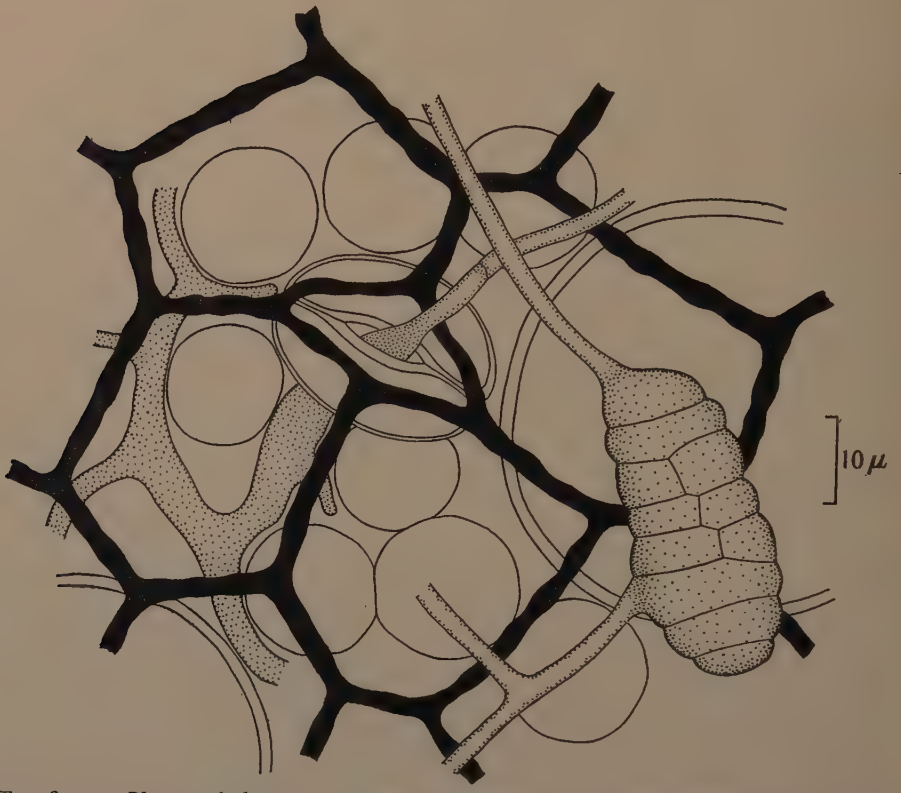
The fungus also flourishes on dead leaves and stems of sainfoin but no ring-spot effect is produced on them. It appears that the spread of hyphae into living tissues is essential for the production of the typical lesion.

The attacked leaflets usually wither and fall, thereby reducing leaf bulk, especially in the spring when the attack is at its height, but on the whole no appreciable damage has been caused to the Glamorgan crops. The ring-spots bear a resemblance to those caused by *Ascochyta Orobi* Sacc., and may well have been confused with them, but examination with a lens will reveal the immersed pycnidia of *Ascochyta* raising the epidermal layer of the diseased tissue. The conidial form of *Pleospora herbarum* has been found frequently in association with the *Ascochyta*.

An aqueous suspension of conidia in an atomizer was used for spraying sainfoin leaves, and ascospores were introduced on to the leaflets as loopfuls of an ascospore suspension. In a very moist atmosphere under a bell-jar in the laboratory, sainfoin plants tend to shed their leaflets for some reason not connected with infection; to avoid this the atmosphere was kept only slightly moist to prevent dropping of the leaflets and to permit infection to take place. After two days the leaflets were removed and boiled in an alcohol acetic acid mixture, stained whole in cotton blue in lactophenol, and mounted in lactophenol as recommended by Smith (1940).

Fungal hyphae from both ascospores (Text-fig. 1) and conidia were seen to have entered the leaf through the stomata but not directly through the cuticle. Cuticular penetration may well take place but it is more difficult to observe. The penetrating hypha, once inside the substomatal cavity, widens considerably and eventually branches and ramifies intracellularly through the leaf tissue. This is almost identical with the description by Smith (1940) of the infection of lucerne by *Pleospora herbarum*, but he apparently observed cuticular penetration of the epidermis also. Fungal hyphae penetrate the epidermal cells from below and finally make their way between epidermal and cuticular layers. Proliferation occurs and subcuticular stromatic cushions are formed (Text-fig. 2). Further proliferation may result in the dissolution or rupture of the outer epidermal wall, with the formation of a deeper and more extensive cushion. The cuticle is torn open and the fungal cells push out hyphae which become thicker and darker walled than the deeper cells, and develop into a tuft of conidiophores. Subsequent development of the conidia has been fully described by Wiltshire (1938). The fungus fruits on both surfaces of the leaflet but more abundantly on the adaxial side.

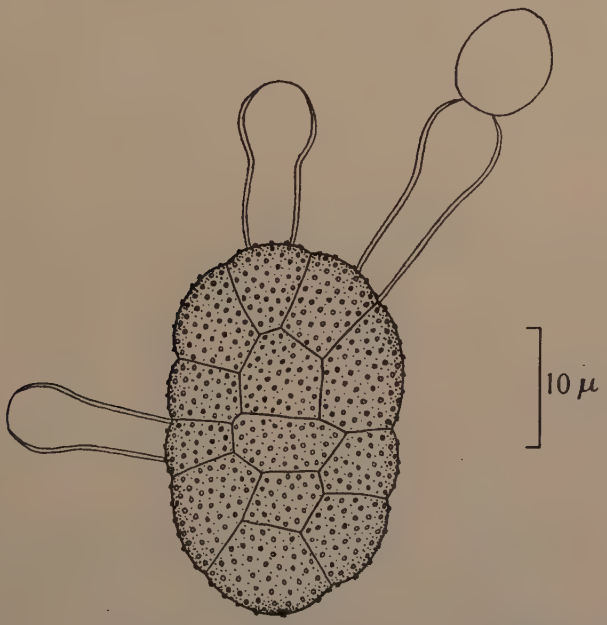
From the form of the conidiophore and conidial characters and measure-



Text-fig. 1. *Pleospora herbarum*. Ascospore germinating on sainfoin leaflet with germ tube penetrating the stomate and swelling in the substomatal cavity. (In the preparation from which the drawing was made, by camera lucida, the penetrating hyphae originated from the ascospore, but for compactness of the figure they are shown unconnected.)

Text-fig. 2. *Pleospora herbarum*. Sectioned leaflet showing production of conidiophores from subcuticular cushion of fungal tissue.

ments, the fungus is referable to *Stemphylium botryosum* Wallroth. The conidial measurements differed somewhat from those recorded by Wiltshire for Wallroth's type specimen. He stated, however, that variation 'may be expected to occur on different hosts in nature and minor differences in spore size alone cannot therefore be regarded as satisfactory ground for maintaining species'. Again, Wiltshire stated that 'confirmatory evidence of the correct identification of the conidial stage is frequently afforded by the development of the ascigerous stage (*P. herbarum*)'.



Text-fig. 3. *Pleospora herbarum*. A conidium producing conidiophores directly.

Portions of cultures from single conidia were planted on rabbit-dung agar with straw added. When these cultures were placed in the light at a temperature of 10–12° C., as advised by Smith (1940), perithecia were produced in abundance. Asci with mature ascospores were formed in about three weeks. It is interesting to note that perithecia of *P. herbarum* were found on dead sainfoin stems in 1942 before any leaf-spotting was observed. Ascospore measurements, obtained from these perithecia, and conidial measurements are given below:

	Substrate	Range	Mean of 25
Ascospores	Dead sainfoin stems	32·4–36·0 × 15·3–17·1 μ	34 × 16 μ
	Dung-agar and straw	31·5–38·7 × 13·5–18·0 μ	35 × 16 μ
Conidia	Dead sainfoin stems	28·8–46·8 × 13·5–20·7 μ	36 × 17 μ
	Leaf-spot on sainfoin	23·4–39·6 × 14·4–21·6 μ	32 × 17 μ

During germination-tests on unmilled sainfoin 'seed', *Stemphylium botryosum* has been frequently met with, growing presumably sapro-

phytically on the pods. Perithecial fundaments developed but did not produce ascospores under the conditions of the test. It is interesting, in view of these facts, to record the finding of a browning and drying-out of one or both cotyledons in a few seedlings from such a sample of seed. *Pleospora herbarum* has been isolated from the diseased tissues, and in a few instances *Botrytis cinerea* Fr.

In Text-fig. 3 a single conidium is shown producing typical conidiophores with a spore initial at the apex of one; this has apparently been noted by the brothers Tulasne (1863) who stated 'we even think we have observed the sarciniform germs produce conidia of the same kind'.

I wish to thank Mr J. Rees for suggesting to me the need of a study of sainfoin diseases. I am also indebted to Mr W. C. Moore for reading the manuscript and for helpful criticisms, and to Miss K. Pears for the photographs.

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EXPLANATION OF PLATE III

A. Infected leaves of sainfoin plants (P_6, Glam. strain) from Experimental Plot, July 1943. The ring-spots are clearly seen.

B. Infected leaves of commercial Hampshire strain of sainfoin from Gileston, March 1944. All stages of infection are shown, from small brown spots to ring-spots. The sooty appearance of some leaflets is evident.

(*Accepted for publication* 24 *January* 1945)

A

B

A LEAF SPOT OF MANGOLDS CAUSED BY *PLEOSPORA HERBARUM* (PERS.) RABENH.

By S. J. HUGHES, *University College, Cardiff*

(With Plate IV)

A spotting of mangold leaves was observed in October 1943 at Llanvaches, Monmouthshire, where the outbreak was reported to have appeared suddenly after heavy rain and general moist conditions.

The spots were circular, 1 mm. to about a centimetre or more in diameter, and on badly infected leaves they coalesced and caused extensive discoloration. The older spots showed concentric rings of light and dark brown regions with well-defined outer margins. Even in the field the fungus produced abundant conidia, giving the spots a sooty appearance. Only *Stemphylium botryosum* Wallroth (*Pleospora herbarum*) was seen on the spots. Leaves at various stages of infection are shown in Pl. IV.

Potash deficiency symptoms were also evident throughout the crop. Some plants were more badly affected than others and showed premature withering of the older leaves, which drooped around the crown like a rosette. The yield of such plants did not appear to be adversely affected as the roots had swollen well, though some had hollow centres; the total yield was estimated at forty tons to the acre. The leaf-spotting developed after the roots were fully grown and would not, therefore, be expected to have reduced the bulk of root. An analysis carried out by Dr W. T. H. Williamson, the Adviser in Agricultural Chemistry, showed that the soil was deficient in potash (exchangeable $K_2O = 0{\cdot}006\%$). This is not unexpected because there had been excessive use of nitrogenous manures, including dung, but only one application of potash, with potatoes, turnips with kale, and mangolds as successive crops.

Whilst most plants showed some leaf-spotting due to *Pleospora herbarum*, the plants suffering from potash deficiency were by far the most badly attacked. The lesions were more numerous and extensive on both green and partly withered leaves, although the innermost and younger unfolding leaves were usually not attacked. These facts suggest that the spot is largely associated with a weakening of the older leaves and also with the deficiency of potash in conjunction with the high nitrogen status.

The fungus obtained from the leaves was *Stemphylium botryosum* Wallroth. Its perfect stage, *Pleospora herbarum*, was obtained in culture on dung-agar and straw, in a good light and at a temperature of 10–12° C. Conidial and ascospore measurements are given below:

	Range	Mean of 25
Ascospores	34·2–41·4 × 14·4–18·0 μ	37 × 16 μ
Conidia	29·7–42·3 × 14·4–23·4 μ	34 × 19 μ

Inoculation experiments were carried out on small, apparently healthy plants taken from the infected field, potted up in soil, and kept indoors under a bell-jar in a moist atmosphere.

Preliminary experiments, using conidia and portions of agar media bearing mycelium, showed no infection if the leaf were undamaged. Ascospores were not available in sufficient numbers to carry out similar inoculations.

Further experiments with conidia and mycelium, on leaves damaged locally by scratching with a needle, showed that infection took place readily, and typical ring-spot lesions were produced. Sections of the diseased leaves showed hyphae of the fungus inter- and intracellularly. *Pleospora herbarum* was re-isolated from the diseased tissues at some distance from the point of inoculation, after sterilizing the surface of the leaves with mercuric chloride solution. When treated similarly, inoculated petioles, previously damaged, were also attacked but the roots remained unharmed.

The fungus *Pleospora herbarum* and its conidial stage *Stemphylium botryosum* have recently been reviewed by Wiltshire (1938). A search through the *Review of Applied Mycology* has revealed that the fungus has a very wide host range; it has been recorded very frequently as the cause of a black mould on onions. Edgerton (1921) concluded that the fungus develops rapidly on any slightly weakened onion tissue, whether mechanically injured or not. Both Edgerton (1921) and Machacek (1929) stressed that great humidity predisposes onions to attack by *P. herbarum*. Such moist conditions prevailed when the mangold leaves were attacked.

Teodoro y Gregorio (1923) recorded positive results after inoculating both injured and non-injured onion leaves but he did not state whether or not they were healthy. On the other hand, *P. herbarum* is recorded by other workers merely as an associate of Downy Mildew (*Peronospora destructor* (Berk.) Casp.); thus, on garlic by Caballero (1922) and on onions by Bremer and Nicolaisen (1934). It is also stated (Cotton, 1922) that *Macrosporium parasiticum* Thüm. (*Pleospora herbarum*) is 'An almost invariable accompaniment of Mildew, and apparently increases the damage caused by *Peronospora*'. There does, indeed, appear to be a measure of doubt as to the extent of the parasitic nature of *P. herbarum* on onions.

Further recorded hosts include lettuce (Ogilvie & Mulligan, 1931; Dippenaar, 1939), *Arctostaphylos manzanita* (Briant & Martyn, 1929), bean seeds (Brinkman, 1931), beetroot (Neuwirth, 1925), apples (Carter, 1935), Clarkia (Lewis, 1937), tomato fruits (Small, 1936), lucerne (Smith, 1940), endive (Moore, 1943) and sainfoin (Hughes, 1945).

Serbinoff (1927), after careful observations in the field and laboratory, concluded that, near Odessa, diseases of cultivated plants caused by species of *Macrosporium* and *Alternaria*, including *M. parasiticum* (*P. herbarum*), are secondary only to attack by different species of bacteria. He regarded the fungus under discussion as either a facultative or a weak parasite.

This paper adds another host to the list of plants capable of being infected by *P. herbarum*. Here, however, the leaf-spotting was probably promoted by a weakening of plant resistance brought on by potash deficiency in conjunction with other unbalanced soil conditions. The *p*H

of the soil was 5·4, which is considered too low for mangold cultivation, but whether or not this affects the resistance of the mangold is not known.

I wish to thank Mr J. Rees, under whose direction the work was carried out, for bringing the disease to my notice. I am indebted to Mr W. C. Moore for reading the manuscript and for helpful suggestions, and to Miss K. Pears for the photographs.

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EXPLANATION OF PLATE IV

Mangold leaves at various stages of infection.

(*Accepted for publication* 24 *January* 1945)

THE TRUE NATURE OF *MYRIOBLEPHARIS* THAXTER

By GRACE M. WATERHOUSE, *Lincoln Training College*

(With Plate V and 4 Text-figures)

When *Myrioblepharis* was found in the Cropston stream, Leicester, by Dr C. T. Ingold and kindly handed over to the Royal Holloway College Botanical Department, it offered a good chance to settle the problem of this genus. The organism was first found there in June 1941 growing on the petioles of decaying alder (*Alnus glutinosa*) and other leaves which had fallen into the stream. Samples have been taken each summer since 1941, and although detailed observations of the time of appearance have not been made, it seems that *Myrioblepharis* usually appears towards the end of June and disappears during late August. A further record of its occurrence was obtained by one of Dr Ingold's students (B. Plunkett), from Evington Brook, south-east of Leicester, in 1943 as late as September. These are the first records of *Myrioblepharis* in the British Isles.

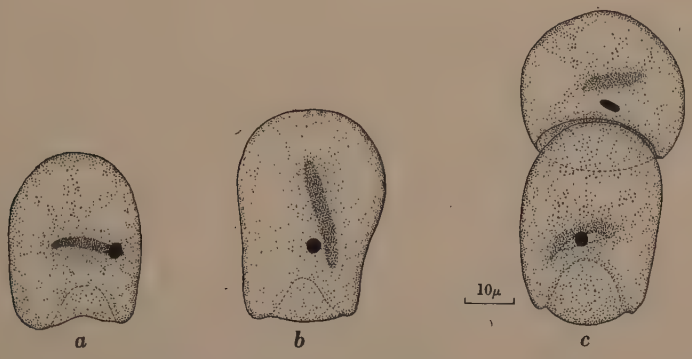
The leaves, at a stage when they were quite brown but not very decayed, were collected from the stream, the laminae were cut off and the petioles washed in tap water and left in open glass dishes in tap water. If examined immediately, specimens of *Myrioblepharis* could usually be seen on a few petioles. Numbers increased considerably in a day or two if left in water (refreshed at intervals).

The status of *M. paradoxa* rests on two descriptions, those of Thaxter and von Minden. The original one by Thaxter (1895) interpreted *Myrioblepharis* as a peculiar genus of aquatic Phycomycetes characterized by multiciliate zoospores but in other respects resembling proliferating species of *Pythium*. Von Minden (1915), however, concluded from his, unfortunately incomplete, observations that there were two organisms present, (1) a *Pythium* of the *P. proliferum* type and (2) a parasitic animal organism —a ciliated protozoan—preying on the sporangia of the fungus. The present investigations which were made in the Royal Holloway College Laboratory in July 1941 and 1942 and at University College, Leicester, in July 1943, establish that von Minden's interpretation was correct: he would doubtless have proved this fully had he been able to complete his observations.

When the petioles collected from the stream were examined, various Protozoa could usually be seen browsing in the tangled web of fungal hyphae, algal filaments and bacteria clothing the surface. One species, rather larger than most, and of a barrel shape, moved about with a slow rolling motion, and it could be seen settling down on the coenocytic hyphae projecting from the substratum. It was this protozoan which proved to be the animal partner of the *Myrioblepharis* association. It was oval or pyriform with a terminal mouth, ciliated all over, and it swam, with the

mouth directed forwards, in a spiral path, rotating about its long axis. It had a single laterally placed contractile vacuole which burst every 6–12 sec. The protoplasm was rather densely granular except in the mouth region where it was clear. Staining showed clearly two nuclei, a large irregular meganucleus and a smaller spherical micronucleus (Text-fig. 1). This feature and the covering of cilia characterize the organism as a member of the class Ciliata of the Protozoa. It has been identified provisionally by Mr A. G. Willis of the Zoology Department of Manchester University as probably a species of *Prorodon.*

The coenocytic hyphae projecting from the petioles were unbranched and grew either in tufts or singly. If unattacked by the ciliate the tufted ones, which were stouter, produced sporangia and zoospores characteristic of proliferating species of *Phytophthora.* The more slender single hyphae produced sporangia and zoospores as in proliferating species of *Pythium.* These were the fungi that the animal used as its hosts. The most detailed

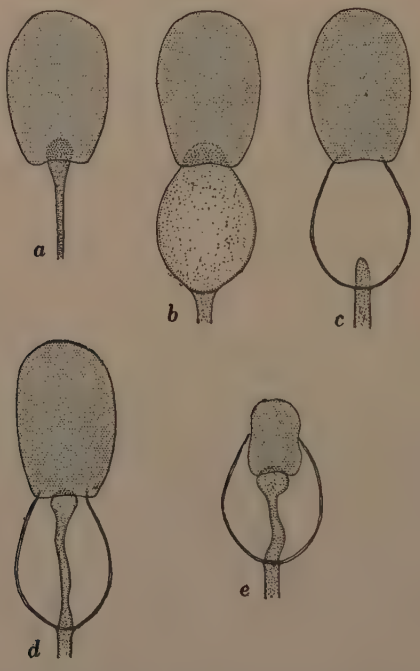


Text-fig. 1. The ciliate showing the meganucleus, micronucleus and mouth; (*a*) young ciliate; (*b*) mature ciliate; (*c*) after the first division. Stained haematoxylin, drawn camera lucida.

observations were made when the ciliate was using the species of *Phytophthora* as host. In the following account therefore, this is the fungus described and figured (Pl. V, figs. 1, 2), but the process when a species of *Pythium* is used as host is essentially the same.

The ciliate always settled down with its mouth over the projecting parts of the fungus (Text-figs. 2, 4), sometimes over a hyphal tip swelling to form a sporangium (Text-fig. 2 *a*, *d*), or over the papilla of a mature sporangium (Text-fig. 2 *b*), or over the opening of an empty sporangium (Text-fig. 2 *c* and Pl. V, figs. 3, 5). Occasionally a young ciliate would squeeze partly into the sporangial opening so that its mouth was over the tip of the hypha proliferating from the base (Text-fig. 2 *e*). As the hypha grew it pushed the ciliate out of and away from the orifice. If the sporangium was nearly mature when the ciliate settled on it, then it dehisced normally, most of the zoospores escaping as the ciliate was pushed away by the swelling vesicle. Some might be trapped in the sporangium as the ciliate settled down on it again. The zoospores were not consumed by the ciliate, indeed, one rounded off almost inside its mouth and could still be seen

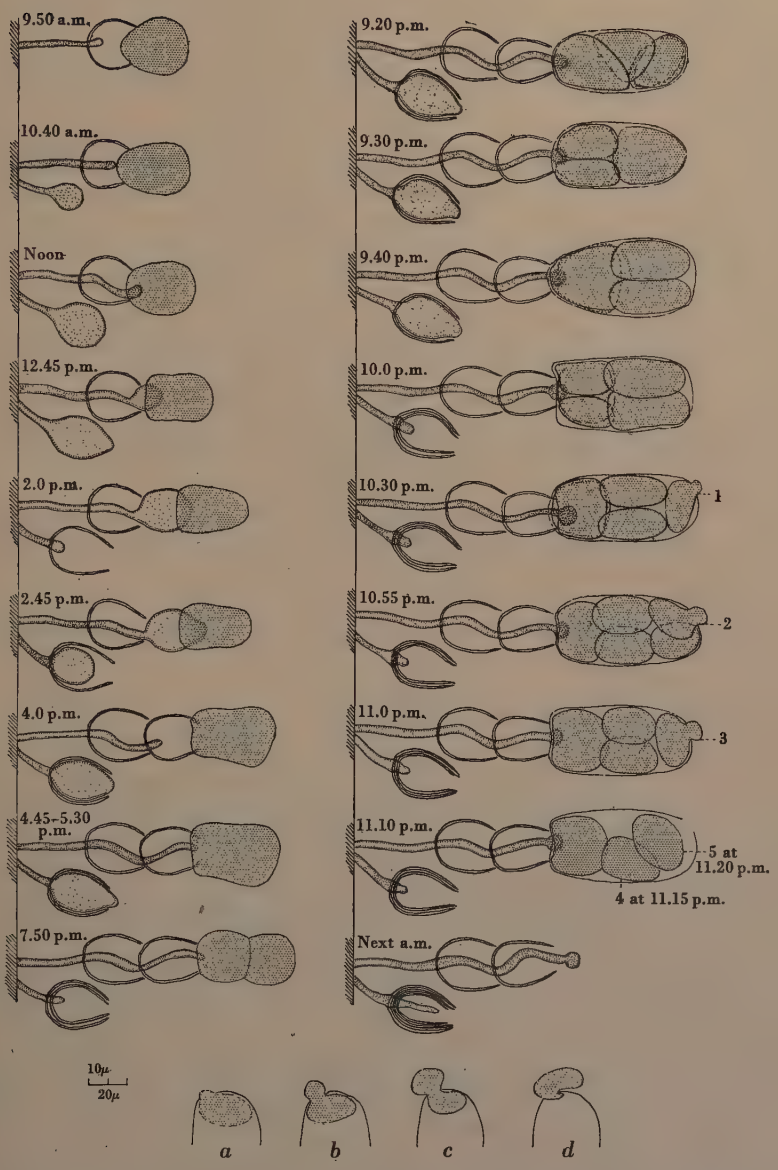
there later. Zoospores were not formed, however, if the ciliate had been in contact with the fungus for any length of time; instead, the contents of the sporangium came out as an undifferentiated liquid mass. This was often seen when the ciliate had been disturbed and had left the sporangium shortly before dehiscence. What happens to the contents when the ciliate remains *in situ* it is not possible yet to say, as a sporangium has not been caught in the act of dehiscence. It is presumed that some or all of the contents pass into the mouth of the ciliate, because sporangia observed



Text-fig. 2. Diagram showing how the ciliate settles mouth downwards on the fungus in different stages of development; (*a*) over the tip of a young hypha swelling to form a sporangium; (*b*) over a mature sporangium; (*c*) over the mouth of an empty sporangium; (*d*) over the tip of a hypha proliferated from the base of an empty sporangium; (*e*) young ciliate squeezed into the opening of an empty sporangium to get its mouth over the swollen hyphal tip. No special magnification. Protoplasm represented diagrammatically by dark stippling in the ciliate and by paler stippling in the fungus.

shortly after emission leave no trace of the contents in the neighbourhood of the opening.

When the organism had settled down on the fungus it became more cylindrical (Text-fig. 4). It rotated slowly; more quickly when fresh water was added. The contractile vacuole could be seen enlarging and suddenly disappearing. Gradually the ciliate grew, and when it reached a certain size (usually after emission of the contents of one sporangium) division took place. A median constriction appeared between the mouth and the posterior end (Text-fig. 4 *b*), indicating that it was about to divide. A young specimen which was watched (in water in an open dish under

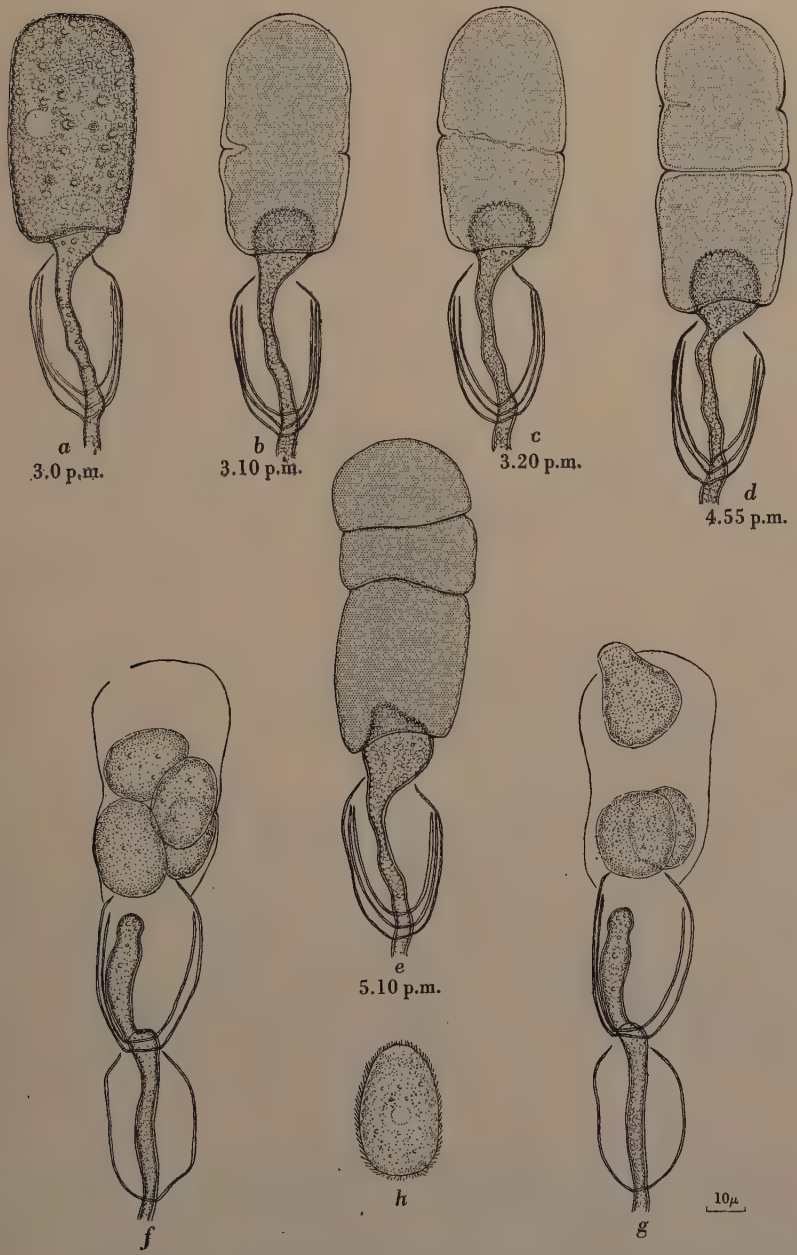


Text-fig. 3. Growth and division of the ciliate and escape of the daughter ciliates produced from the division; 9.50 a.m.–4.45 p.m. growth of young ciliate; 7.50–10.20 p.m. divisions of ciliate; 10.30–11.10 p.m. escape of the products (order of escape 1–5). An uninfected fungus sporangiophore grew up at the side and produced three successive sporangia which dehisced normally. *a–d*, escape of first daughter ciliate through pore in cyst. Drawings camera lucida. Protoplasm shown diagrammatically as in Text-fig. 2. Substratum shown diagrammatically.

the microscope) during its development took about eight hours to reach this stage of division (Text-fig. 3). In the course of the next hour cleavage into two was completed. Cleavage began with a dip in the cuticle, and a few minutes later cleavage of the outer region of the protoplasm could be seen. This proceeded inwards until the protoplasm was cut in two (Text-fig. 4 *c*). In one specimen this division took twenty minutes. During division the contractile vacuole was not seen and rotation usually ceased. Then followed a quiescent period of an hour or more during which the organism (both halves) grew. A second cleavage, similar to the first, then took place but only in the posterior half (Text-fig. 4 *d*, *e*). Rotation sometimes began again at this stage, each part moving independently. The two posterior ones or even all three might swim away, especially if disturbed, but usually further divisions followed (Text-fig. 3). These divisions were difficult to see owing to the density of the protoplasm and movement of the products. It was not possible to see in what plane the final divisions occurred, but it seems probable from knowledge of division in ciliates generally that the subsequent cleavage planes were parallel to the first. The four products of the third division became so disposed that two lay posterior to the other two. Sometimes five daughter ciliates were ultimately produced from the upper half. How the division proceeded to produce the fifth could not be seen. When the organism was fully divided the products lay within a pellicle or cyst and moved there for some time before they escaped (Text-fig. 4 *f*, *g*). A pore was formed in the cyst and the daughters squeezed through one by one. The young ciliate thus produced was about 9–12 μ long and pyriform, the narrower anterior end being clearer than the rest of the protoplasm (Text-fig. 4 *h*). It swam for a short time only before settling down on the fungus and restarting the cycle. The anterior half of the organism which remained in contact with the fungus sometimes swam away as well or else it remained to grow and divide again or sometimes it seemed that it divided at the same time as the posterior half.

The sequence of events was thus very much as Thaxter described it. The most conspicuous difference was in the speed of the changes taking place. The time taken for the fully grown organism to segment and discharge its products was only half an hour in the North American material, whereas in the English material it was six hours. Thaxter commented on the speed and violence of the rotating movement. It was evidently the rapidity of growth and movement which obscured the details and led Thaxter to interpret the products of division as the zoospores of the fungus. He did at first consider that he had an epizooic or ectoparasitic creature but later discarded the idea.

This account is given to show that *Myrioblepharis* is really two organisms, viz. a fungus and a protozoan. It does not elucidate the relationships between the two, as more observations will be necessary before this can be done. Is the animal using the fungus merely as a convenient perch while it divides, or is it absorbing nutriment from the fungus? Facts which point to the latter view are (1) that the ciliate settles with its mouth over the hyphal tip, (2) it grows while it is situated there, (3) the contents of



Text-fig. 4. *a–e*, stages in the division of the ciliate; (*a*) mature ciliate with its mouth over a developing sporangium of the fungus, revolving slowly, contractile vacuole showing; (*b*) first sign of cleavage in ciliate, movement has ceased, no contractile vacuole evident; (*c*) first cleavage complete; (*d*) beginning of second cleavage; (*e*) second cleavage complete; movement then began again and all three parts swam away 5.25 p.m. *f–g*, escape of daughter ciliates; (*f*) one daughter has already escaped through a pore in the cyst; (*g*) young ciliate escaping through pore; (*h*) young ciliate after escaping. Camera lucida. Protoplasm shown diagrammatically by stippling in *b–e*.

the sporangium, although not seen to pass into the animal, were not to be found in the vicinity soon after emission (von Minden stated that the entire contents were emptied into the revolving body), (4) after the ciliate has rested on the sporangium for a time it fails to produce zoospores but instead gives out a mass of protoplasm: this suggests that the ciliate is affecting the fungus adversely although not necessarily absorbing substance from it, (5) the newly formed ciliate has a very short swimming phase before it settles down on the fungus.

The species of both *Phytophthora* and *Pythium* used as hosts have been grown in culture but have not yet been identified. One would like to isolate the ciliate in culture too and then reunite the partners to produce the *Myrioblepharis*. It is probable that so specialized a ciliate might not live in culture. The cultured fungus, however, might be reinoculated with the ciliate from the stream at the appropriate time of year. Even without these final proofs it can be said definitely that *Myrioblepharis* as a genus is no longer valid, although one might refer to the *Myrioblepharis* association which occurs between a ciliate and some aquatic species of *Pythium* and *Phytophthora* at a certain time of the year.

Summary

Evidence is brought together whereby the long-suspected double nature of *Myrioblepharis paradoxa* Thaxter is finally demonstrated. What may now be termed the *Myrioblepharis* association is provided by a ciliate and a species of either *Pythium* or *Phytophthora*.

I acknowledge with gratitude the help given by Miss E. M. Blackwell and by Professor C. T. Ingold, particularly for the photographs which he took and which are used for Plate V.

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EXPLANATION OF PLATE V

Figs. 1, 2. Typical sporangia of the species of *Phytophthora* used as host.

Fig. 3. Mature ciliate over the mouth of an empty sporangium, the fungus hypha is proliferating from below and swelling to form another sporangium. The ciliate shows signs of division.

Fig. 4. First division of the ciliate in process while situated over a mature sporangium. To the right a young ciliate on a sporangium.

Fig. 5. Ciliate fully divided into three, lower half with a slight constriction prior to division; situated over an empty sporangium with the proliferating hypha grown up into the mouth of the ciliate.

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STILBUM TOMENTOSUM SCHRAD.

By T. PETCH

Historical

This fungus, a common parasite of *Trichia* and other Myxomycetes, was described by Schrader (1799) as '*Stilbum tomentosum*, stipite tomentoso, capitulo subrotundo'. Schrader stated that it grew on *Trichia* and other allied species, and also on sheep dung, first appearing as a small white tomentose patch, from which there soon arose a slender stalk, clothed with similar tomentum, the specific epithet being chosen because of the tomentum on the stalk. It is to be noted that, as Schrader stated that it grew on *Trichia* and on sheep dung, he evidently confused two different fungi. His enlarged figure of a specimen on a *Trichia* shows a glabrous stalk.

Persoon (1801) quoted Schrader's name and description, with the alternative name, *parasiticum*, and suggested that the tomentum was some *Byssus* which had developed on the stalk during drying, and hence the name *parasiticum* would be more suitable.

Albertini and Schweinitz (1805) recorded *Stilbum tomentosum* Schrad. on *Trichia*, *Cribraria vulgaris*, *C. cernua*, etc., and noted that in their specimens both the tomentum on the stalk and the subiculum on the host were always present.

Ditmar (1817) adopted the name *Stilbum parasiticum* Persoon. He stated that the stalk was glabrous, and that the hyphae observed by Schrader, which occurred sometimes, but not always, at the base of the stalk, appeared to him to be an intrusive mould, as its varying occurrence would seem to indicate. He gave figures of the fungus growing on '*Trichia nitens* Persoon', and his enlarged figure shows the stalk minutely rough.

Persoon (1822) listed it as '*Stilbum parasiticum*, stipite glabro, tomentulo insidente', adding that the stalk was glabrous but arose from a byssoid subiculum, and noting that Albertini and Schweinitz had recorded that they had always found the stalk tomentose. He did not, as has been stated, distinguish two forms, but merely adopted his previous alternative name.

Greville (1827) described the stalk of *S. tomentosum* as glandulose, set with minute pellucid rounded processes or glands, and the conidia as very minute, globose. He added: 'It is true, that in some specimens a fine delicate mucor-like substance is said to envelope the whole plant; but that is an extraneous appendage. In its natural state, it is completely destitute of any such appearance.' Greville (1823) had previously described, on *Trichia*, *Isaria microscopica*, a very minute species, in which he was unable to find conidia. Fries (1829) suggested that the latter was immature *Stilbum tomentosum*, and that view has been generally accepted.

Fries (1829) adopted Schrader's name, describing the fungus as having a tomentose stalk united to a byssoid mycelium, with a form *b*, stalk yellowish, somewhat glabrous, which he suggested was an older state. For

the type he cited Schrader (1799), Persoon (1801), Albertini and Schweinitz (1805), and Greville (1827), and for form *b*, Ditmar (1817) and Persoon (1822).

Berkeley (1836) gave to *Stilbum tomentosum* the English name, glandular *Stilbum*, and described the stalk as glanduloso-tomentose, recording it on *Trichia fallax* and *T. chrysosperma*.

Saccardo (1886) cited Schrader, Greville and Ditmar for this species, and described the stalk as glanduloso-tomentose, arising from a byssoid base. He did not give any spore measurement.

Oudemans (1886) recorded *Stilbum parasiticum* Pers. on *Trichia chrysosperma*, and stated that the flocci on the stalk described by Schrader were completely lacking in his specimens. Later (1903) he declared that the woolly surface of the stalk, on which Schrader based the name of the species, was not due to glands, as many authors had supposed, but to hyphae of the central column which bend outwards and bear each an apical conidium. Apparently it did not occur to him that those hyphal tips might be the glands of previous authors. Oudemans gave the conidia as globose, hyaline, 1·2 μ diameter, but in view of his statement it is uncertain whether he measured the glands on the stalk or the conidia on the head.

Massee (1893) gave the conidia as globose, 2–3 μ diameter, while Bresadola (1903) stated that they were 4–5 × 2–2·5 μ. The question of the size of the spores was dealt with by Miss A. L. Smith (1903) who wrote as follows:

'My interest in the fungus was aroused by the difference in the form and size of the spores, which puzzled me in my attempts to classify various specimens. The stalk I have always found to accord with Greville's description, "set with minute pellucid roundish processes". The spores in Greville's and Ditmar's figures are small rounded bodies. Saccardo describes them as "globosis, exiguis", and Massee, in his *Fungus Flora*, adds the exact measurement as 2–3 μ diameter. Specimens sent to me from Hampshire and Devonshire tally with the above descriptions; the stalks are beset with processes, the spores are globose, though smaller somewhat. They are extremely minute. I received still another specimen from Egham, in Surrey, which had a similar stalk, but the spores are oval in form and measure up to 5 × 2 μ. On examining *Stilbum tomentosum* in the National Herbarium at South Kensington, I found a Ceylon specimen in the Broome collection, in which the spores have been drawn and measured by that careful worker; they are oval in form and 0·0002 in. long, or 5 μ. There are other specimens in the Broome herbarium collected in England, but the spores are not figured. The difference between the two kinds of *Stilbum* amounts almost to a specific distinction, but the plants are otherwise so much alike that it seems better to distinguish the second as a variety. The form with globose spores has priority, the other I propose to name var. *ovalisporum*.'

Examination of the specimens in Herb. Mus. Brit. shows that the data have been confused, probably in writing up the notes. The slide of the Hampshire specimen is marked by Miss Smith, 'elliptical spores', and has oval spores about 5 μ long; the *Stilbum* is on *Trichia varia*, and was gathered at Alresford, Hants, March 1902, by the Rev. W. Eyre: another head from

this collection gave conidia 3–4·5 × 1–1·5 μ. The slide of the Egham specimen is marked, 'on *Trichia* from Egham with round spores'; it is on *Trichia varia*, and the head of the *Stilbum* is covered with a mass of minute granules; it is mounted in glycerine. Another slide from a specimen from St Catherine's shows minute oval conidia with acute tips, 0·75–1 × 0·5 μ, or globose conidia, 0·5 μ.

The Ceylon specimen referred to by Miss Smith is on *Hemitrichia serpula*, Thwaites no. 130. There is another Ceylon specimen, Thwaites no. 83, in Herb. Mus. Brit., on which Broome has drawn the conidium as oval, 0·00015 in., that is, 3·75 μ, though in the *Fungi of Ceylon*, no. 1003, the measurement was given as 0·0003–0·0004 in., or 7·5–10 μ. Measurements on fresh specimens on *Trichia Botrytis* in Ceylon gave in one case 1·5–2 × 0·75 μ, and in another 1·5–3 × 0·75–1 μ. But on examining the part of Thwaites no. 83 which Thwaites retained in the Peradeniya herbarium, I found that it bore conidia which attained a length of 10 μ or more. These, however, were not the conidia of the *Stilbum*. The latter was in turn parasitized by a hyphomycete which consisted of a few hyaline septate hyphae, about 3 μ diameter, twining round the *Stilbum* stalk and head and producing solitary oval *Cephalosporium* heads, up to 13 × 7 μ, each containing up to eight conidia in a parallel bundle, the conidia being hyaline, cylindrical, 10–12 × 2 μ, with some only 4–5 μ long. That was tentatively referred (Petch, 1912) to *Cephalosporium stellatum* Harz (1871), recorded as parasitic on *Stilbum bulbosum* and *S. vulgare*, but when comparison with Harz's original figure and description was possible, it was seen that that identification was wrong, if Harz's figure is correct. That, however, is immaterial to the present discussion, the relevant point being that the long conidia observed on the Ceylon specimen, Thwaites no. 83, are those of a hyphomycete parasitic on *S. tomentosum*.

Berkeley and Broome (1873) found on *Hemitrichia serpula*, Thwaites no. 83, a perithecial stage which they described as *Hypomyces stilbiger*, and they added to their description the note, 'It is very interesting to ascertain that *Stilbum tomentosum* Schrad. is merely the conidiophore of a *Hypomyces* parasitic on *Trichiae*'. This species now stands as *Byssostilbe stilbigera* (B. & Br.) Petch (1912). I have collected it in Ceylon on *Trichia Botrytis* and *T. affinis*, and it has been recorded from Java as *Ophionectria* (*Ophiostilbe*) *Trichiae* Penz. & Sacc. I have not seen any indication of this species on any British specimen of *Stilbum tomentosum*, nor have I found any record of its occurrence elsewhere. Bommer and Rousseau (1884) gave *Hypomyces stilbiger* as the perithecial stage of *Stilbum tomentosum*, but they were merely quoting from Berkeley and Broome.

Stilbum tomentosum has been found in Ceylon on *Hemitrichia serpula*, *Trichia varia*, *T. affinis* and *T. Botrytis*, and is especially common at Hakgala on the last-named species. The stalks are always glandular, and usually arise from the sporangia without, or with only a slight, basal mycelium. Small white isolated patches of mycelium generally indicate perithecia.

Specimens of *Stilbum tomentosum* in herbaria are often unserviceable, as the head is easily broken off when dry. Conidia have been found on the following specimens in Herb. Kew.

'Queen's Cottage Grounds, Kew', n.d.; on *Trichia varia* and *T. affinis*; heads not found; specimen on *T. varia* bears loose conidia, cylindrical, ends rounded, 8–10 × 2–4 μ, and oval conidia, 4 × 1·5–2 μ, lying together.

'On *Trichia clavata*, Shere, October 1866, D. Capron'; is on *T. varia*; no conidiophores on stalk or base; conidia oval, 1·2–2 × 0·75–1 μ, a few globose, 1 μ.

'E. Vize, *Microfungi Britannici*, 354, Forden'; on *Trichia varia*; conidia oval, ends rounded or subacute, 4–6 × 2 μ.

'On *Trichia affinis*, Eastham Rake, 14 January 1911, Herb. Dr J. W. Ellis'; is on *T. varia*; no conidiophores on stalk or base; conidia in the head oval, 2–4 × 1–1·5 μ; a loose cluster of subcylindrical conidia, 8–10 × 2–2·5, and another group, subcylindrical, narrow oval or fusoid, 4–6 × 2 μ.

'Thwaites no. 83, Peradeniya [Ceylon], November 1867'; on *Hemitrichia serpula*; conidia oval, ends acute or obtuse, 2·5–4 × 1–1·75 μ. It is to be noted that *Hypomyces stilbiger*, which is also Thwaites no. 83, was collected in December 1868.

'On *Trichia Botrytis*, Hakgala [Ceylon], May 1910, no. 257'; conidia in the heads rod-shaped, ends rounded, 3–4 × 0·5 μ; subcylindric conidia 9–12 × 1·5–2 μ also present.

The differences thus far revealed in the published descriptions and the herbarium specimens relate to the character of the stalk and the dimensions of the conidia. But Grimm (1889–90) had raised another question. He had found *Stilbum tomentosum* common in the neighbourhood of St Petersburg, and had grown it in culture. He stated that, about a month after sowing the conidia, small cushions appeared, consisting of a mass of united vertical hyphae, which produced branches with terminal conidial *Cephalosporium* heads over the whole surface of the cushion. This structure increased in height, and then the hyphae branched at the apex, the branches producing similar conidial heads which fused into a globose terminal head. Grimm figured the fungus on *Cribraria argillacea*, *Dictydium umbilicatum* and *Arcyria cinerea*, and stated that the conidia were 9 × 4 μ. His figure shows an isarioid structure with suberect *Cephalosporium* conidiophores, each with its separate head of conidia, diverging from it, and a large globose terminal head of conidia.

Apparently, Grimm's paper passed unnoticed until it was taken up by Lindau (1909), who, on the facts given therein, transferred *Stilbum tomentosum* to *Tilachlidium*, as *T. tomentosum* (Schrad.) Lind. Lindau gave the conidia as cylindrical, obtuse, 3·5–7·5 μ long, 2–2·5 μ broad, rarely almost globose, 3·5 μ diameter, though he quoted Grimm's measurement, 9 × 4 μ, in his summary of the latter's paper. He added that while Oudemans found, laterally on the stalk, only conidiophores with a single apical conidium, Grimm under more favourable conditions found conidiophores with complete *Cephalosporium* heads. He did not recognize that Oudemans' conidia on the stalk were probably the glands, and that Grimm's conidia are something quite different. What had become of the glands in the structure Grimm obtained is not recorded. Meanwhile it may be said that nothing similar to Grimm's fungus has been observed to occur on Myxomycetes in nature, and it is doubtful whether it should be regarded as a

Tilachlidium. The type of the latter genus is a solid, simple or branched clava, with *Cephalosporium* conidiophores more or less perpendicular to the stem, not an isarioid group of diverging conidiophores.

Ferraris (1909, 1910) objected to Lindau's transference of this species to *Tilachlidium*, and stated that after examining numerous examples he had not been able to find the lateral heads described and figured by Grimm. He gave a figure of the stalk with its minute projecting hyphal ends, the glands, and described the conidia as typically very minute, obovate, $1{\cdot}2 \times 0{\cdot}5\mu$, or subglobose, $1{\cdot}2\mu$ diameter, or in the variety *macrospora* Ferr., founded to distinguish the form recorded by Bresadola, $3–5 \times 2–2{\cdot}5\mu$. The latter is apparently var. *ovalisporum* A. L. S.

Von Höhnel (1916) transferred *Stilbum tomentosum* to *Dendrostilbella*.

Recent observations

An extensive growth of *Stilbum tomentosum* on *Trichia varia* and *T. persimilis* on the under-side of a fallen trunk on swampy ground was found in Holt House Wood, near King's Lynn, 3 April 1930. The *Stilbum* fructifications were up to 1·75 mm. high, with a stalk up to 0·25 mm. diameter, and a head up to 0·36 mm. diameter, or larger by fusion with adjacent synnemata. In some instances the stalks were branched, a decumbent stalk giving rise to erect lateral branches of the same character as the parent.

The stalk is invariably composed of parallel agglutinated hyphae, and sparsely or densely covered with minute spore-like bodies. Some of the latter are globose, up to 4μ diameter, and these are usually lateral and sessile on the exterior hyphae of the stalk; others are oval, up to $8 \times 4\mu$, and these are either lateral, like the globose bodies, or are the projecting tips of the stalk hyphae. All these bodies are hyaline and minutely verrucose, and in some specimens the exterior hyphae of the stalk are also minutely verrucose. These spore-like bodies are no doubt the 'glands' of Greville, and probably the one-spored conidiophores of Oudemans; they are typical of *S. tomentosum* and are figured by Ferraris, but except for some of the oval bodies there are no free hyphal ends and the stalks are not tomentose in the usual sense.

The young synnemata, before the formation of the head, have, as a rule, no white basal patch, and the smaller mature synnemata either lack a basal patch or have a small repent fleck of mycelium at the base which is scarcely discernible until the specimen is mounted. The larger and older specimens in this collection had a visible white basal patch. The repent hyphae of this patch bear lateral sessile spore-like bodies, like those of the stalk.

The conidiophores in the head are narrow flask-shaped or conical, $12–16\mu$ long, $1{\cdot}5\mu$ diameter below. In very small heads they arise from the apices of the fused hyphae of the stalk, but in the larger heads the stalk hyphae separate above and the conidiophores arise in clusters of up to four from the apex of a stalk hypha, with sometimes a single conidiophore from the first node below. In general, the flask-shaped conidiophore has a short neck, about 3μ long, on which the conidium (oval in these specimens) is

sessile, but in some instances the thin apex is produced to double that length and terminates in a globose body about 1 μ diameter. It is possible that the latter is a developing conidium, but it is not quite what one would expect. Measurements of the conidia from nine heads gave the following: oval, ends acute, 3–5 × 1·5 μ (a small head); narrow oval or oblong-oval, ends obtuse, 5–8 × 2–2·5 μ; 4–7 × 2–3 μ (five synnemata from the same sporangium); 4–6·5 × 1·5–2 μ; 4–6 × 1·5–2 μ. It is possible that some of these were mixtures, as will be explained later. Chains of conidia were not observed.

Well-developed basal patches bore *Cephalosporium* conidiophores, up to 50 μ high, 2 μ diameter below, tapering regularly upwards. The *Cephalosporium* head, in general, was oval, about 10 × 7 μ, containing conidia in parallel, but some globose heads, with irregularly placed conidia, were found. The conidia in these heads were oblong-oval, obtuse, 5–8 × 2–3 μ. As a rule, these conidiophores arose from the white basal patch, quite independent of the regular glandular stalk. From a group of conidiophores round a broken *Stilbum* stalk, in which the conidia were 5–8 × 2·5–3 μ, one conidium was found, oblong-oval with obtuse ends, 12 × 4 μ.

In the following year (17. 10. 1931) two collections of *Stilbum tomentosum* on *Trichia varia* were made from the same log as the previous specimens. One was taken as possibly something different, as the *T ichia* sporangia were black and the *Stilbum* heads translucent when fresh, but the stalks were normally glandular and the conidia narrow oval, 3–5 × 1·5 μ, the larger with acute tips, the smaller obtuse. A culture was made from this gathering, and repeated transfers were made during the next five years. The *Stilbum* grew quite normally on oatmeal agar, with the typical glandular stalk and narrow oval conidia, with ends subacute, 3·5–5 × 1·5–2 μ, sometimes 6 × 2 μ.

In the second collection of the same date, the sporangia were yellow and the *Stilbum* heads opaque, many synnemata terminating in a small pencil of conidiophores with conidia, 3–4 × 1·5–2 μ. A *Cephalosporium* conidiophore from the basal mycelium of one synnema was 65 μ high, 1·5 μ diameter below, with conidia oblong-oval, 7–10 × 2–3·5 μ.

Seven other collections made at various times on *Trichia varia*, *T. affinis*, and *Perichaena populina* had conidia, 3–6 × 1·5–2 μ, occasionally 7 μ long. I have found the typical form with minute conidia on three occasions only, viz. on *Trichia decipiens*, Mulgrave Woods, 16 September 1930, conidia globose, 0·75–1 μ diameter, a few oval, 1 × 0·75 μ; on *T. persimilis*, Barnard Castle, 18 September 1933, conidia globose, about 1 μ diameter, or oval, 1·5 × 1 μ; on *T. affinis*, Duncombe Park, Helmsley, 31 August 1935, conidia globose, about 1 μ diameter, but some oval conidia, up to 9 × 3 μ also present. I regret that I did not take any of these into culture, probably because I was under the erroneous impression that I could obtain this form at any time nearer home.

In October 1934, gatherings of *Stilbum tomentosum* were made in Norfolk on *Cribraria rufa*, *C. argillacea* and *Comatricha pulchella*. In these, gathered in wet weather, the sporangia were bound together by mycelium. In one synnema, from *Cribraria argillacea*, the stalk terminated in a convex head,

surmounted by a distinct cap composed of moderately crowded *Cephalosporium* conidiophores, each with its separate globule of conidia, which were oblong, obtuse, sometimes curved, 5–7 × 1·5–2 μ. In another synnema from *Cribraria rufa*, *Cephalosporium* conidiophores were present on the stalk, with oblong or oblong-oval conidia, 4·5–7 × 2–3 μ. A culture was made on oatmeal agar from *Cephalosporium* conidia on the mycelium of the latter specimen. No *Stilbum* synnemata were produced in this culture, but scattered or crowded groups of *Cephalosporium* conidiophores, with a ring of separate conidiophores at the margin of the culture. The conidiophores were branched at the apex, with a single branch below, but not definitely acrostalagmoid; each branch bore a globule of oblong-oval, oval or cylindrical conidia, 5–11 × 2–3 μ.

Of nineteen recent British collections of *Stilbum tomentosum* made between 1930 and 1938, only three were the form which has been considered typical, that with minute conidia, either globose, 0·75–1 μ diameter, or oval 1–1·5 × 0·75–1 μ. The others were all var. *ovalisporum* A. L. Sm. (var. *macrospora* Ferr.), with oval conidia, usually 3–5 × 1·5–2 μ. Both forms are often parasitized by a *Cephalosporium*, which has oval, oblong-oval or cylindrical conidia, 5–12 × 2–4 μ, and the large spores which frequently occur in mounts of *Stilbum tomentosum* belong to the *Cephalosporium*. The stalks of both forms of *S. tomentosum* are minutely glandular as described by Greville; a tomentose stalk usually indicates that the specimen is parasitized. Extensive basal mycelium is usually that of the parasite, but unparasitized specimens have a slight basal mycelium, especially when old.

It would appear that Grimm cultivated the *Cephalosporium*, as his figures show *Cephalosporium* heads and he gave the dimensions of the conidia as 9 × 4 μ. His fungus was apparently a tuft of *Cephalosporium* conidiophores, not *Stilbum tomentosum*. Von Höhnel (1916) stated that *Tilachlidium* was a *Cephalosporium* coremium, but that is rather an over-simplification, unless he got his idea of the genus from Grimm's figure. In any case, Grimm's results do not warrant the transference of *Stilbum tomentosum* to *Tilachlidium*.

The descriptions of the genus *Tilachlidium* and its type species, *T. pinnatum*, are somewhat confusing, because Preuss described the *Cephalosporium* conidiophores as branches. Amalgamating the two descriptions, *Tilachlidium pinnatum* had a white or pallid simple clava, composed of agglutinated hyphae, covered everywhere with spreading *Cephalosporium* conidiophores, the conidia being ovate-oblong, hyaline, dimensions not stated; it occurred on effete agarics, especially *Mycena galericulata*. Miss A. L. Smith (1909) described another species, *Tilachlidium subulatum*, on plant debris, the clavae being gregarious, erect, yellowish or greyish white, covered everywhere with *Cephalosporium* conidiophores, which Miss Smith's figure shows more or less perpendicular to the clava, with cylindrical conidia, about 5–7 × 2 μ. From the descriptions these two species appear to be the same.

In 1937, I pointed out that *Isaria brachiata* (Batsch) Schum. was a *Tilachlidium*, but did not 'make the combination'. The name was published as *T. brachiatum* (Batsch) Petch in *Trans. Norfolk and Norwich Nat. Soc.* (1940), xv, 198. The fungus was originally described by Batsch (1786) as

Clavaria, and occurs principally on decaying agarics, but sometimes on vegetable debris, though there is a possibility that in the latter instances some unrecognizable agaric remains may be present. It has a wide distribution, and I have examined specimens from Britain (Yorks and Norfolk), the U.S.A. and Mauritius. The clavae usually occur in clusters, and are white to pale brown, simple or branched. As figured by Batsch, the branches sometimes leave the main stem at unusual angles and are narrowest at the point of attachment, while they are sometimes again similarly branched. The branches and the main stem are covered with spreading *Cephalosporium* conidiophores, simple or branched, usually perpendicular to the stem or branch. The conidia are cylindrical or narrow oval, hyaline, 2–7 (usually 3–6) × 0·75–1·5 μ. *Tilachlidium pinnatum* and *T. subulatum* appear to be merely the simple form of *T. brachiatum*.

Tilachlidium is not merely a *Cephalosporium* coremium, that is, it is not composed of hyphae which separate and curve outwards at different heights, each terminating in a *Cephalosporium* head. It has a solid stem, tapering to an acute apex, and composed of parallel agglutinated hyphae which do not separate. The *Cephalosporium* conidiophores are not hyphal tips, but arise perpendicularly from the exterior hyphae of the stem. Grimm's figure is not a *Tilachlidium*.

If the type specimen of *Corethropsis epimyces* Massee (1885) is available, it might be worth while examining it to ascertain whether it is not *Tilachlidium brachiatum*. It occurred on decaying *Mycena pura*.

Summary

Two forms of *Stilbum tomentosum* occur, one, taken as the type, with minute conidia, the other, var. *ovalisporum* A. L. Sm. (var. *macrospora* Ferr.), with conidia, 2·5–5 × 1·5–2 μ. The latter appears to be the commoner in England. Both have glandular stalks.

Both forms are frequently parasitized by a *Cephalosporium*, which has conidia, 5–12 × 2–4 μ.

Grimm cultivated the *Cephalosporium*. The fructification he obtained in culture was apparently a tuft of *Cephalosporium* conidiophores, not *Stilbum tomentosum* nor a *Tilachlidium*.

Isaria brachiata (Batsch) Schum. is a *Tilachlidium*, *T. brachiatum* (Batsch) Petch (1940). *T. pinnatum* Preuss and *T. subulatum* A. L. Sm. appear to be the simple form of *T. brachiatum*.

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INVESTIGATION INTO THE PRODUCTION OF BACTERIOSTATIC SUBSTANCES BY FUNGI

CULTURAL WORK ON BASIDIOMYCETES

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Fungi which have produced bacteriostatic substances of therapeutic importance have usually belonged to the genera *Aspergillus* and *Penicillium*. In this Laboratory some 150 species and strains of the former and some 200 species and strains of the latter genus have been investigated with more or less gratifying results (Wilkins & Harris, 1942, 1943*a*, 1944*b*, 1944*d*). More recently, attention has been paid to the production of such substances by the larger Basidiomycetes and of the 780 species which have been examined about 10% were strongly and about 20% weakly antibacterial in action (Wilkins & Harris, 1944*c*). Though positive results were less frequent in the Basidiomycetes than in the two first mentioned genera there appears to be justification for further investigation. Species of *Aspergillus* and *Penicillium* present little cultural difficulty, they grow rapidly on a variety of solid and liquid media and can be tested with reasonable accuracy by the method devised by the author. The Basidiomycetes, on the other hand, present, in addition to the difficulty of isolation, special difficulties in culture. Many will not grow satisfactorily on any medium, solid or liquid, that has yet been tried; many are extremely specific to certain media; while many others grow so slowly as to be useless as a means of producing anti-bacterial substances in anything approaching a reasonable time. This paper deals with experimental work which attempts a solution of at least some of the difficulties involved. It has been assumed that the sporophores themselves could not be regarded as a reliable source of anti-bacterial substances in the therapeutic sense, hence the object was to induce the fungus to grow on a liquid medium and produce a metabolism solution which could be tested as to its effect on bacteria and from which the anti-bacterial substances (if any) could be chemically extracted, thus following the line adopted in the case of the 'moulds' mentioned above. Of the total number of 780 Basidiomycetes which had been tested as extract, fifty-six were isolated in culture. These were not specially chosen but just happened to be those which were available for collection and which were successfully grown in culture, and some had given a positive and some a negative result when tested as sporophore extract. These cultures were grown on a variety of different solid and liquid media but it was found that the media most favourable for growth were the three that had been found most satisfactory for species of *Aspergillus* (Wilkins & Harris, 1944*d*), viz. Potato dextrose, Malt and Czapek-Dox. Considerable attention was paid to methods for ascertaining rapidly whether a fungus might be regarded as promising

without, if possible, going through the lengthy process of growing it on the liquid medium. This will be referred to later. The methods which were used for testing the bacteriostatic properties of these Basidiomycetes were three. (1) Freshly gathered sporophores were squeezed or ground and the 'juice' or extract was tested by the 'hole' method mentioned above (Wilkins & Harris, 1943). This was the preliminary (and usually the only) test which was applied to the 780 species already tested. (2) The fungus was isolated in pure culture on an agar medium and tested by the mycelial 'disc' or 'strip' methods (Wilkins & Harris, 1944, 1944*a*). (3) The fungus, having been isolated, was grown on liquid media and the metabolism solution was tested by the standard 'hole' method already mentioned. Whether tested by the extract, strip or liquid methods, each fungus was tested against two representative types of bacteria, *Bacterium coli* and *Staphylococcus aureus*. In accordance with previous experience of the non-susceptible reaction of *Pseudomonas pyocyanea* to most Basidiomycetes, this bacterium was not used.

The following list shows the results of testing the fifty-six fungi which have been isolated as, (1) extract, (2) strip, and (3) liquid. In the last two cases, for the purposes of comparison, the fungi were grown on each of the three media mentioned. Sub-cultures of most of the fungi have been deposited with the Lister Institute and the number following the name of the fungus is the Lister Reference Number. In the list the symbol 'X' indicates a positive and the symbol 'O' a negative result. The symbol '—' indicates that mycelial growth was so slow that no test could be made within any reasonable time limit, and a complete blank means that no test was made. The letters PD, M and CD stand respectively for potato dextrose, malt and Czapek-Dox media. Under each test the results are in pairs, the first symbol in each pair represents the action against *B. coli* and the second symbol of the pair shows the action against *Staphylococcus aureus*, e.g. 'O.X' indicates negative against *B. coli* and positive against *S. aureus*.

List of fungi tested

		Strip			Liquid		
	Extr.	PD	M	CD	PD	M	CD
Armillaria mucida 6900	O.O	O.O	O.O	O.O	O.O	O.O	O.O
Boletus bovinus 6905	O.O	O.O	O.O	O.O	O.O	O.O	O.O
Clitocybe aurantiaca 6879	X.O	O.X	O.X	O.X	—.—	O.X	—.—
C. cerussata 6924	O.O	O.O	O.O	O.O	—.—	—.—	—.—
C. clavipes 6902	O.X	O.X	O.O	O.O	O.O	O.X	O.O
C. diatreta 6918	O.O	O.O	O.O	O.O	X.X	X.X	—.—
C. flaccida 6904	O.X	O.X	O.X	O.X	O.X	O.X	O.X
C. geotropa 6886	O.O	O.O	O.O	O.O	O.O	O.O	O.O
C. infundibuliformis 6913	O.O	O.X	X.X	O.O	X.X	X.X	—.—
C. inversa 6878	X.X	O.X	X.X	O.X	O.X	X.X	O.X
C. nebularis 6940	O.O	O.X	O.O	O.X	X.X	O.O	—.—
C. odora 6901	O.X	O.X	X.X	X.X	—.—	X.X	—.—
C. vibecina 6936	X.X	X.X	X.X	O.X	O.X	O.O	—.—
Clitopilus prunulus 6911	O.X	—.—	—.—	—.—	O.X	O.X	—.—
Collybia butyracea 6882	O.O	O.O	O.O	O.O	O.O	O.O	O.O
C. fusipes 6908	O.O	O.O	O.O	X.X	O.X	X.X	—.—
Coprinus atramentarius 6899	O.O	O.O	O.O	O.O	O.O	O.O	—.—

List of fungi tested (continued)

	Extr.	Strip PD	Strip M	Strip CD	Liquid PD	Liquid M	Liquid CD
C. comatus 6892	O.O	O.O	X.O	O.O	O.O	X.X	X.O
C. picaceus 6888	O.O	O.X	O.X	O.X	O.O	O.X	O.X
Crucibulum vulgare 6955		—.—	—.—	—.—	O.X	O.X	O.X
Flammula sapinea 6893	O.O	O.X	O.X	O.O	O.O	O.X	—.—
Hebeloma crustuliniforme 6938	X.X	—.—	—.—	—.—	O.O	O.O	O.O
Hygrophorus eburneus	X.X	—.—	—.—	—.—	X.O	O.O	—.—
H. pratensis 6954		O.X	O.X	X.X	O.X	O.X	O.O
Hypholoma fasciculare 6898	O.O	O.O	O.O	O.O	O.O	O.O	—.—
Lepiota procera 6894	O.O	O.O	O.O	O.O	—.—	—.—	—.—
L. rhacodes 6887	O.O	O.O	O.O	O.O	O.O	O.O	—.—
Marasmius alliaceus 6880	X.X	O.O	O.O	O.O	O.O	O.O	O.O
M. conigenus 6890	O.X	X.X	X.X	O.X	X.X	X.X	O.X
M. oreades 6906	O.O	O.O	O.O	O.O	O.O	O.O	O.O
M. peronatus 6885	O.O	O.O	O.O	O.X	O.O	X.O	—.—
Mycena galericulata 6937	O.O	O.O	O.O	—.—	—.—	—.—	—.—
Naucoria pediades 6909	O.O	X.O	O.O	X.O	O.O	O.O	X.O
Omphalia umbilicata 6920	X.X	O.X	O.X	O.O	O.X	O.X	—.—
Panus stipticus 6903	O.X	O.X	O.O	O.O	O.X	O.O	O.O
Paxillus involutus	O.O	—.—	—.—	—.—	—.—	—.—	—.—
Pholiota aegerita 6939	O.O	O.O	O.X	X.X	O.O	O.X	O.X
Pleurotus sapidus 6910	O.O	O.O	O.O	O.O	O.O	O.O	O.O
Polyporus betulinus 6891	O.X	X.O	O.O	O.O	O.X	O.O	O.O
Polystictus versicolor 6895	O.O	O.O	O.O	O.O	O.O	O.O	O.O
Psalliota arvensis 6889	X.X	X.X	X.X	O.O	X.X	X.O	X.O
P. campestris 6916	O.O	O.O	O.O	O.O	O.O	O.O	—.—
P. haemorrhoidaria 6915	O.O	—.—	—.—	—.—	O.O	O.O	—.—
P. pratensis 6925	O.O	O.O	O.O	O.O	O.O	O.O	—.—
P. sylvatica 6914	O.O	O.O	O.O	—.—	O.O	O.O	—.—
P. sylvicola 6912	O.O	O.O	O.O	—.—	O.O	O.O	O.O
P. villatica 6917	O.O	O.O	O.O	O.O	O.O	O.O	—.—
P. xanthoderma 6921	X.X	X.X	X.X	X.O	X.O	O.O	—.—
var. *grisea* 6923	X.X	X.X	X.X	X.O	O.O	X.O	—.—
var. *lepiotoides* 6897	X.X	X.X	X.X	O.O	X.X	O.O	O.O
var. *obscurata* 6922	X.X	X.X	X.X	O.O	O.O	O.O	—.—
Stropharia aeruginosa 6896	O.O	O.O	O.O	O.O	O.O	O.O	O.O
Tricholoma grammopodium 6877	O.O	O.O	O.O	O.O	O.O	O.O	O.O
T. nudum 6935	X.X	X.X	X.X	X.X	X.X	O.X	O.X
T. personatum 6876	X.X	X.X	X.X	—.—	O.X	O.O	—.—
T. sordidum 6919	O.X	X.X	X.X	X.X	O.X	O.O	—.—

From the above it is at once apparent that the action against *Staphylococcus aureus* is more frequent than that against *Bacterium coli*. It is in fact rare to find an action against *B. coli* only. This confirms previous findings.

It is also obvious that the choice of medium is an important factor. Potato dextrose and malt are, in general, equally suitable but rarely are both equally favourable for the same fungus. In most cases potato dextrose gives rather wider zones than does malt, though this fact is not indicated in the above results. Liquid Czapek-Dox gives poor results, many of the fungi will not grow on it and in any case the results on this medium are never as high as on either of the other two. Czapek-Dox agar, on the other hand, is more satisfactory all round, *Collybia fusipes* for instance, would not grow on the liquid but in the strip test the CD agar was the only medium that gave a positive result. Four years of experience have repeatedly suggested that the composition of the substrate, either as an artificial

medium or in natural habitat, is perhaps one of the most, if not the most, significant factor in the production of bacteriostatic substances by fungi, and this question is being systematically investigated.

The determination of a method to indicate whether a fungus is likely to produce anti-bacterial substances in quantity and in a reasonable time, though not wholly satisfactory, has met with some measure of success. It was at first hoped that a positive sporophore extract would give a positive metabolism solution and vice versa, but the following figures from the list show that this is not entirely reliable:

Numbers of fungi that are		
Positive in extract	Negative in liquid	Positive in liquid
22	2	20
Negative in extract		
32	22	10

Those that are positive in extract are, with two exceptions, which may again be due to medium complications, positive in liquid culture, but in the case of those which are negative in extract the chances of their being negative in liquid culture are only two to one, and it would be undesirable to lose possible good 'positives' to the extent of 30% of those tested.

Because the above difficulty had been a constant source of anxiety the 'disc' and 'strip' methods of testing were devised. It was realized that there was considerable difference between what might be expected from a squeezed sporophore and what might result from the same fungus grown in culture, but it was hoped that between a fungus grown on an agar medium and the same fungus grown on a similar liquid medium, there would be some similarity of reaction. The following figures show some justification for this idea:

Numbers of fungi that are		
Positive in strip	Negative in liquid	Positive in liquid
28	0	28
Negative in strip		
28	24	4

Here it seems that if a fungus gives a positive result in the strip test it will give a positive result when grown in liquid and, if the strip test is negative, approximately 90% of the liquid tests will be negative also. Though discouragingly large it might be that the discrepancy was due to experimental error but, in any case, this method, which has the advantage of being simple and rapid, is the most satisfactory yet devised.

The question of strain variation which was examined in *Aspergillus* (Wilkins & Harris, 1944*d*) presents itself here. It was found that individuals of the same species collected from different localities gave results which were constant for any given locality but which varied from strongly positive to negative according to the locality from which they were collected. As these results were based almost entirely on sporophore extract alone, further statement is postponed until investigations now in hand are completed.

Conclusions

The evidence to date suggests that the larger Basidiomycetes are significantly productive of the anti-bacterial substances and merit further investigation. It appears that, contrary to original expectation, the testing of the sporophore extract alone, though to some extent indicative, is not wholly reliable as a test for a positive result in the ultimate metabolism solution. It seems to be essential to isolate the fungus into culture when a strip test will, in the majority of cases, give a reasonably satisfactory indication as to what might be expected from liquid culture. Strain variation, i.e. in the present sense the variation of individual fungi, still requires elucidation and is being further investigated.

To my Research Assistant, Dr G. C. M. Harris, who has now left to take up another appointment, I am grateful for valuable help with the above work.

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A ROOT ROT OF CINERARIA, AND A STUDY OF THE SPECIES OF *PHYTOPHTHORA* CONCERNED

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Introduction

Cinerarias were grown to a considerable extent in Ayrshire nurseries for the pot plant trade before the war. Many nurserymen annually lost an appreciable proportion of their stock as the result of a root-rot disease associated with wilting of the leaves. This disease appeared at all stages in the growth of the Cineraria, but the periods when plants were most susceptible were during the seedling stage and just prior to flowering.

Isolations made from fragments of diseased root tissue almost always resulted in a culture of a phycomycetous fungus resembling a species of *Phytophthora*.

Review of previous work

Few records exist of research into the cause of a Cineraria Root Rot. The only direct references to a naturally occurring Root Rot ascribed to *Phytophthora* are those of Pethybridge and Lafferty (1919) in Britain, and in Victoria (Australia) of Brittlebank and Fish (1927), who name as the causal organism *P. cryptogea*. Tomkins, Tucker and Gardner (1936), working on a Cauliflower Root Rot caused by *P. megasperma*, reported the same fungus present on Cinerarias affected with Root Rot. Symptoms of wilting were artificially induced in Cineraria by Tomkins and Tucker (1937) using an isolate of *P. cryptogea* from China Aster. In 1935 Drechsler recorded *Pythium* on Cineraria roots, though the fungus was not isolated.

Symptoms

The disease is first apparent when the aerial portions of the Cineraria show a tendency to wilt. The lower leaves are affected first, while still retaining their green colour; later the young leaves droop. First the laminae become flaccid, then the petioles loose their turgidity. The central axis of the plant usually remains upright. The condition appears suddenly in 1–2 days.

In severe attacks shading and watering failed to produce any recovery. When sun heat became more intense and pots dried out, some plants showed a tendency to wilt more readily than others. These were probably plants in which fungal invasion was still not far advanced, and they were capable of recovery when shade and water were provided. The infected plants, however, remained less tolerant of extremes than plants free from disease.

When wilted plants were shaken from their pots, a pinkish coloration of the roots, in contrast with the white roots of healthy specimens, was a

constant feature, though sometimes it appeared only in patches. In advanced stages of the disease the roots were brown and a soft odourless rot was evident. The cortex sloughed easily on pulling the root from the soil. In the crown of the plant, rotting of the xylem and pith was frequently involved.

These symptoms appeared on both *Cineraria stellata* and *Cineraria grandiflora*.

Isolation of the causal organism

Roots which showed the pinkish discoloration of the stele were selected from diseased plants at different stages of development. These were cut into short lengths, surface sterilized in 0·1 % mercuric chloride and plated on potato agar. Fungal growth was observed after 2–3 days.

The fungi isolated included species of *Fusarium* and on three occasions *Ascochyta*, but most of the platings produced, usually as the only growth, a phycomycetous fungus resembling either *Pythium* or *Phytophthora*. It is difficult to distinguish between these genera, but the presence in some of these Phycomycetes of amphigynous oogonia, and the tendency to release zoospores directly from the sporangium with no external vesicle, suggests that the genus is *Phytophthora*. From March and throughout the summer, all but one of the diseased plants whose roots were plated produced *Phytophthora* cultures.

In view of the ease and frequency of *Phytophthora* isolations, sometimes appearing as pure cultures, it seems most likely that isolates of this genus are the cause of Root Rot of the Cineraria.

Proof of pathogenicity

Artificial inoculations of healthy plants were carried out using pure cultures of several isolates, grown on crushed oats, cracked wheat, or potato agar. The inoculum was introduced into the soil near the roots of healthy plants. Injury to plant roots was avoided as much as possible by knocking the plants out of their pots and pushing pieces of culture into the side of the soil ball. As a rule 3–5 points of infection were introduced into the root ball of each plant in a $4\frac{1}{2}$ in. pot. The Cinerarias were then replaced in their pots without further root disturbance.

The plants, with controls, were kept in a slightly heated greenhouse and given ample root moisture.

As a result of these inoculations 64 % of the plants produced wilt symptoms and root rot. Some of the isolates attacked more readily than others but all were capable of producing symptoms of Root Rot. The disease usually became apparent in four weeks, and sometimes the symptoms could be distinguished in eight or nine days.

Roots from artificially infected plants were surface sterilized and plated on potato agar; these again yielded *Phytophthora* cultures.

Description of the isolated species

Five isolates of *Phytophthora* obtained from five wilted plants grown in Ayrshire were labelled F_2, G_1, H_1, J_2 and R_1.

These isolates when cultured on a variety of media, showed considerable variation.

On potato agar

On plates of this medium H_1 produced a prostrate spreading mycelium, hyaline and of an even density, and close, rapid growth. The hyphae were coarse, infrequently branching and occasionally septate; their diameter was 4–7 μ.

The mycelium of isolates J_2, R_1, F_2 and G_1 bore more resemblance one to another; all produced a small amount of thin aerial mycelium over the prostrate, spreading, hyaline growth. At 20° C. the increase in diameter was much slower than that of H_1. Microscopically the mycelia of J_2, R_1, F_2 and G_1 showed a close resemblance. Hyphae branched almost at right angles, and the young branches were of a similar diameter to the hyphae from which they arose. For the most part the hyphae were coenocytic, but septa were found in older hyphae of all four isolates. The average diameter of the hyphae was 5·5 μ, but this was not constant throughout the length. In some parts the hyphae appeared to be distended and in others constricted. A constriction occurred particularly at the point of origin of a lateral branch from its parent hypha. None of the cultures produced spores.

On oatmeal agar

Profuse growth developed on plates of oatmeal agar at 24° C. The aerial mycelium of isolates R_1, H_1, G_1 and J_2 was abundant, white and flocculent; that of F_2 was less plentiful. The incidence of reproductive organs was variable. The mycelia of F_2, R_1 and J_2 were purely vegetative after 6 week's growth. That of H_1 bore irregularly shaped granular bodies which might have been sporangia. The mycelium of J_2 bore thin-walled intercalary swellings.

In Petri solution

Tucker (1931) found that some species which rarely produce sporangia on solid media could be induced to form them in Petri solution. Tubes of this solution were inoculated with pieces of agar culture of F_2, G_1 and H_1. After incubation at 24° C. for five weeks the mycelia of F_2 and G_1 remained vegetative. In the culture of H_1 some very small bodies, 11 μ in diameter, resembling sporangia were found.

On plugs of Cineraria tissue

In the taxonomic keys relating to *Phytophthora* (Tucker, 1931; Leonian, 1934) the form of the antheridium, whether amphigynous or paragynous, is a major feature in classification. If sexual organs could be induced to form, they would prove a useful means of differentiation between the strains and an aid to identification of the species. Since the isolates showed no tendency to form reproductive organs on artificial media, it seemed possible that they required a substratum more closely resembling the host plant for their development.

Stems of *Cineraria stellata* were cut into convenient lengths to fit into test-tubes, and split lengthwise to expose the soft inner tissue on which the fungus may grow more readily. Sterilization was carried out at 1 atm. for 20 min. Two days later the plugs were inoculated with all five isolates and incubated at 24° C.

No growth was produced by J_2. Abundant flocculent mycelium formed in 4 days on plugs inoculated with H_1, in 6 days from R_1, in 10 days from F_2, and in 14 days a slight weft developed from G_1 with very small beaked or papillate sporangia.

Sexual organs were infrequent. The first to be observed were found on F_2, two weeks after inoculation of the plug. The oogonia were golden brown, smooth-walled and spherical, drawn out slightly within the amphigynous antheridia. The oogonia measured 25–29·7 μ in diameter or 37 μ to the base of the antheridium. Oospores measured 18·6–22·3 μ diameter. A later inoculation failed to produce oogonia until after a 13-week interval when the plug had almost dried out. Oogonia were then found in abundance.

The only other isolate to form oogonia was R_1. On this culture after 5 weeks there were many golden brown oogonia, 25·5–30 μ diameter, with amphigynous antheridia. The other isolates showed no sexual stage.

Sporangial formation

The transference of the fungus from a highly nutritive substratum to a liquid medium of low nutritive value has been found to have the effect of inducing members of this genus to form sporangia (Pethybridge & Lafferty, 1919). This method was applied to the isolates from Cineraria in three ways.

(1) Well-nourished aerial hyphae were taken from agar cultures, avoiding where possible any fragment of the agar substratum. F_2, G_1 and H_1 were taken from oatmeal-agar cultures and J_2 from potato agar. Tubes of sterile distilled water were inoculated with this vigorously growing material.

In 2 weeks' time H_1 had formed spherical thin-walled sporangia in abundance. F_2 produced sporangia after seven weeks more typical of the genus *Phytophthora*. These were elongate-ovoid, somewhat irregular in outline, measured 22·2–15 × 11–7·5 μ, and had granular contents. The other isolates, G_1 and J_2, remained vegetative. Oval intercalary chlamydospores were found on the mycelia.

(2) Five isolates were grown on a highly nitrogenous medium consisting of potato agar to which 1 % KNO_3 had been added (pH 5·5). After a few weeks' growth, subcultures were made in liquid bog soil extract (pH 4·6). The tubes were incubated at 20° C. for three weeks before examination.

Isolate F_2 under this treatment produced no sporangia comparable with those induced by transference to distilled water. A few intercalary swellings were present. G_1 bore a few small ovoid sporangia on very strong hyphae. Intercalary swellings of this isolate were seen to be germinating in situ, one or more hyphal tips emerging from all sides of a single swelling. J_2 formed large ovoid sporangia, quite distinct from the intercalary swellings which were also present and which germinated similarly to those of G_1.

R_1 and J_2 both formed large ovoid sporangia in culture; those of R_1 measured $44{\cdot}4 \times 25{\cdot}8\mu$. Intercalary swellings germinating in all directions by hyphal protuberances were present in groups. H_1 produced no true sporangia, but some short lateral hyphae were abnormally swollen, making 'thumb-like' projections from the main hyphae.

(3) Leonian's technique (1934), involving the transference of cultures from pea broth to distilled water, was followed in order to encourage sporangial development in the present isolates, with these results:

F_2. Occasional sporangia, oval non-papillate; av. $30{\cdot}6 \times 21{\cdot}6\mu$.

J_2. Occasional sporangia, oval non-papillate; av. $31{\cdot}5 \times 21{\cdot}5\mu$.

H_1. Round intercalary sporangia.

R_1. Vegetative.

From the cultural work it was apparent that the isolates varied widely in their reaction to different media. Although a *Phytophthora* species could be isolated without difficulty from Cineraria plants with wilt symptoms, in each case an apparently different strain was obtained. Each showed distinctive reactions to cultural treatments distinguishing it from other isolates.

Similarly, when reisolates from artificial inoculation were grown in culture, it was found that some of these differed slightly in behaviour one from another and also from the strains which were introduced into the plant, yet all were apparently species of *Phytophthora*.

The presence of ovoid non-papillate sporangia of the type associated with the genus *Phytophthora* has been recorded for F_2, G_1 (very small), H_1 (very small), J_2 and R_1, though each produced the organs under different conditions. Oogonia with antheridia were found only in isolates F_2 and R_1.

The marked dissimilarity in behaviour suggested that more than one species may be present on Cinerarias affected with Root Rot. Reproductive structures, however, were so few and infrequent that it was difficult to identify the species by morphological features alone.

So far the isolates seem to fall into three groups:

F_2, R_1. Each formed oogonia with amphigynous antheridia and had large sporangia.

J_2. Similar sporangia were present but no growth developed on Cineraria plugs. The sexual stage was not observed.

G_1, H_1. These isolates produced very small sporangia.

Attempts to classify the Cineraria isolates

Keys to identification compiled by Tucker (1931) and Leonian (1934) are based on (*a*) the response of the organism to culture on certain media, notably by the production or absence of sexual organs or sporangia; (*b*) the tolerance of the species to extremes of temperature or concentrations of malachite green; and (*c*) differential pathogenicity on potato tubers.

Cultures on various media have been made and the resulting growth compared in a previous section. Subsequently experiments were carried

out to determine the pathogenicity on potato tubers, and the tolerance of the isolates of varying temperature and of concentrations of malachite green. In addition, trials were made to indicate the range of *p*H which would support the growth of the various isolates.

Pathogenicity on potato tubers of *Phytophthora* isolates from Cineraria

Cultures of the fungus on potato agar were used for inoculation of the tubers. Potatoes were washed and, after surface sterilization with alcohol, three V-shaped incisions were made equidistantly spaced on three sides of each. The flap of tissue so made was raised and a piece of agar inoculum bearing the *Phytophthora* was introduced underneath. Each potato was thus inoculated three times with the same isolate. Controls were tubers similarly cut but not inoculated. The tubers were kept moist under inverted sterilized bell jars and incubated at 24° C.

Results

J_2. After 6 days the tissue surrounding all inoculated lesions had turned brown and rotted, while all control cuts remained healthy. The isolate was pathogenic to potato tubers and was reisolated from the lesions.

R_1. Two inoculations proved pathogenic in seven days. All controls remained healthy.

F_2. All inoculations proved pathogenic after seven days.

G_1, H_1. After 20 days, inoculated cuts still remained healthy. A thin callus formed on the tissues lining the cut. These two isolates were inoculated into a second series of tubers and again they were non-pathogenic.

The relationship between temperature and growth of Cineraria isolates

Plates of potato agar (*p*H 5·8) were inoculated with the five strains of *Phytophthora* derived from Cineraria plants. The inoculum was of uniform size and planted in the centre of the plate to allow of equal growth on all sides. The plates were incubated at temperatures ranging from 16 to 35° C. Once set, the incubators maintained a fairly steady temperature.

Recordings of the mean diameter of growth were made after 96 hr. For each strain there is an upper temperature limiting to growth. F_2 was inhibited at 30° C. G_1 and J_2 produced a trace of growth at 30° C. but failed to grow at 32° C. R_1 gave measurable growth at 30° C. but also failed to grow at 32° C. H_1 made vigorous growth at 32° C., but at 35° C. was inhibited. In each case the limiting effect of increased temperature acted rather suddenly; vigorous growth was brought abruptly to an end by an increase of 1–2°.

The effect of low temperatures was also tried. In this case potato-agar plates were incubated at 24° C. for one day, in order that initial growth might develop in the fresh agar. The circumference of growth was outlined on

the under glass of the Petri plates before the series was transferred to a cold room, with a temperature of 8–9° C.

The growth of H_1 at this low temperature was the most rapid. F_2 grew slightly. The development of R_1 and J_2 was scarcely perceptible.

Differential growth in malachite green solution

Leonian (1934) found that the response of different species to the presence of small amounts of malachite green in the growth medium was a fairly constant specific character on which classification within the genus might be based. His cultures were in a liquid medium, the formula for which was closely followed in this work except for the substitution of Witte peptone for the proteose peptone used by Leonian. His technique for dissolving in it minute quantities of malachite green was also employed. Dilutions containing 1 part of dye in 2, 3, 4, 8 and 12 millions were prepared. Tubes were selected for uniformity in diameter and shape. The media were tubed (5 c.c. per tube) and sterilized, and after a few days were inoculated. Inoculum was cut from potato agar plates of the various Cineraria isolates, using a sterilized platinum wire bent to form three sides of a 1 mm. square. In this way the size of inoculum used in each tube could be made nearly identical. One piece of inoculum was introduced into each tube, and each treatment repeated four times. The tubes were kept at 20° C., and after two weeks they were examined and the amount of growth measured and recorded.

The concentration of 1 in 3 millions prevented the growth of all the isolates. F_2 and G_1 would tolerate a concentration of 1 in 4 million. J_2 was more sensitive, and only one plate at the concentration of 1 in 8 million showed a trace of growth; even at 1 in 12 million growth was slight. H_1 was the most sensitive of all, even the most dilute solution of the dye inhibited its growth.

Review of results

A study of the foregoing experiments dealing with the effects of temperature and different concentrations of malachite green on growth, and with pathogenicity for potato tissue, indicates that there is a tendency, among the isolates of *Phytophthora*, to group themselves in a manner which is repeated in each experiment. Isolates J_2, F_2 and G_1 repeatedly show a very similar growth response to a range of temperatures. H_1 produces wider growth and tolerates higher temperatures than other isolates.

On malachite green media, again the responses of isolates F_2, G_1 and J_2 approximate more closely than the others. R_1 resembles this group, but in a later experiment R_1 was slightly more tolerant than other isolates in that group. H_1 is distinct from all the others.

In pathogenicity tests on potato tubers, once more the resemblance held between F_2 and J_2. Isolate R_1 joins this group, and these produce disease within 7 days. H_1 was non-pathogenic. G_1, usually with the former group, this time falls into the latter, as it has been found to be non-pathogenic.

A further series of experiments dealing with the response of the isolates

to varying degrees of acidity was carried out to find if a similar grouping exists under these conditions.

The effect of varying pH on the Phytophthora *isolates from Cineraria*

Potato-agar medium of a series of *p*H values was prepared, adjusting the acidities by means of solutions of $Na_2HPO_4 . 12H_2O$ and pure citric acid to obtain the range of *p*H values 3·67, 4·19, 4·59, 5·96, 6·39, 6·68 and 7·17.

Three plates of each *p*H value were inoculated with each of the *Phytophthora* strains F_2, J_2, H_1 and R_1 and incubated for four days at 23° C. At the end of that time the diameter of growth was measured and the results tabulated.

From a study of the results it appeared that over a wide range of *p*H, the effect on strains F_2, R_1 and J_2 was small. With a 2·3 increase in acidity (*p*H 6·4–4·1) the decrease in diameter growth was no more than 4–5 mm. As the acidity increased beyond *p*H 4·1 there was a sharp decrease in growth. At *p*H 6·68 there was a decrease in the growth of all isolates, but it increased again as the *p*H exceeded 7·0. The growth of H_1 filled the plate at *p*H values from 4·5 to neutrality.

Again the grouping of the isolates follows the previous tendency, F_2, J_2 and R_1 showing similarity in behaviour and H_1 behaving independently. In a previous experiment in which G_1 was included the graph for the development of G_1 closely followed that of isolates F_2, J_2 and R_1.

Reinoculation of Cineraria plants

The cultural work carried out with isolates of *Phytophthora* from Cineraria suggests that these include more than one species. The behaviour of isolates F_2, J_2 and R_1 show so close a similarity under all treatments given as to be considered a single species. G_1 reacted in the same way to temperature, acidity and the presence of malachite green, but was non-pathogenic on potato tubers. Except for this one response the strain resembled the previous ones. H_1 differed consistently from other isolates.

In order to determine whether one or all of these groups is responsible for the disease, artificial inoculations of healthy plants were made at intervals during all seasons of the year.

The results of the inoculations are here tabulated.

Strain	Successful inoculations	Incub. days	Delayed symptoms	Incub. weeks	Unsuccessful inoculations	Total	% success
R_1	10	7–32	1	15	—	11	100
J_2	5	6–25	3	6–17	1	9	89·0
F_2	8	8–28	—	—	4	12	66·7
G_1	5	8–40	2	6–14	4	11	63·6
H_1	3	17–35	1	10	7	11	36·3

R_1 proved to be the most virulent strain. J_2, F_2 and G_1 produced symptoms less readily, and H_1 occasionally produced disease but was less virulent.

Identification of the strains

An attempt was made to determine the species of the five isolates of *Phytophthora* by means of the keys drawn up by Tucker (1931) and Leonian (1934). To these were related the results of cultural work already described in this paper.

R_1. The isolate R_1, of which the life history is most complete, showed a spreading growth on agar media at 20° C., and the maximum temperature for growth was 30–31° C. No oogonia developed on oatmeal agar or on any other agar medium tested, but they appeared, with amphigynous antheridia, on tissue plugs. Sporangia, formed in a soil extract, were non-papillate.

From these features the fungus might be identified, according to Tucker (1931), as one of the following species:

P. erythroseptica, *P. Richardiae*,
P. Cinnamomi, *P. cambivora*,
P. cryptogea.

It can be distinguished from *P. erythroseptica* by its smaller oospores, i.e. less than 30μ in diameter. Its pathogenicity on potato tubers, its smaller sporangia, and optimum growth below 25° C., distinguishes it from *P. cambivora*.

The pathogenicity on potato tubers and absence of oogonia on oatmeal agar distinguish it from *P. Richardiae*. There remains, therefore, *P. cryptogea* and *P. Cinnamomi*.

Intercalary swellings developed in a culture transferred to bog-soil extract. The presence of these vesicles, rare in *P. cryptogea*, together with the lack of sexual organs on oatmeal agar, suggest that the isolate is *P. cinnamomi*.

Transference of a pea-broth culture to distilled water failed to produce any sporangia or sexual organs, though some hyphal swellings developed. Restricted growth continued in the presence of 1 in 8 million malachite green. From these additional features Leonian (1934) would classify the isolate as *P. Cinnamomi*. Thus the previous conclusion, based on Tucker's classification, is confirmed.

J_2. The behaviour of J_2 closely resembled that of R_1. Temperature relations were the same. Aerial mycelium formed on oatmeal agar and no oogonia were observed. Sporangia were of similar dimensions to those of R_1. Intercalary vesicles, germinating by hyphal tips, formed in bog-soil extract cultures of J_2 also. J_2 was pathogenic on potato tubers. These two isolates might be regarded as the same species, but oospores of J_2 were not observed. Provisionally, therefore, J_2 will be classed with R_1 as *P. cryptogea* or *P. cinnamomi*.

The nature of growth of distilled water after three days in pea broth, on which Leonian based his key, does, however, reveal a difference between J_2 and R_1. J_2 produced a very few scattered sporangia. This feature points to the isolate being *P. citrophthora* (Leonian, 1934). This is unlikely since the sporangia of the isolate are non-papillate, and the temperature relations recorded by Tucker (1931) do not agree. On account of the rare occurrence

of these sporangia J_2 might well be classed with the group in which they are absent, thus resembling R_1. It would then be classified as *P. cinnamomi*.

F_2. The temperature relations and the behaviour of this isolate on potato agar were similar to those of R_1, and it was pathogenic on potato tubers. Non-papillate sporangia and oogonia with amphigynous antheridia were formed. The oogonia measured 25–30 μ in diameter. Hence, according to Tucker (1931), the identity of the isolate might be:

P. cryptogea, *P. Richardiae*,
P. cambivora, or *P. Cinnamomi*.

From *P. Richardiae*, the isolate can be distinguished by temperature relations (*P. Richardiae* failed to grow at 10° C. (Tucker, 1931)), by pathogenicity on potato tubers, and by the size of oogonia (those of *P. Richardiae* are greater than 35 μ in average diameter).

The pathogenicity of F_2 on potato tubers, together with the smaller sporangia and its optimum growth below 25° C., distinguish it from *P. cambivora*.

The dimensions of sporangia and oogonia found in F_2 cultures conform more closely to *P. cryptogea*. The absence of oogonia on oatmeal-agar cultures, however, and the presence of groups of vesicles on cultures of F_2 suggest that this isolate again is *P. Cinnamomi*.

According to Leonian's key, the production of sporangia in sterile water after transference from pea broth together with the toleration of 1 in 8 million malachite green would classify this isolate as *P. citrophthora*. Again, as with isolate J_2, it is probable that since the production of sporangia is occasional, the fungus might be identified as *P. Cinnamomi*.

G_1. The behaviour of the vegetative mycelium of G_1 was very similar to that of R_1 and J_2. No aerial growth was formed. The temperature range was the same as that of R_1 and J_2. Intercalary vesicles, germinating by hyphal tips, were again present. In the reproductive structures no similarity could be traced. No oospores were observed, and the only sporangia which could be induced were very small. The isolate was not pathogenic on potato tubers. It is suggested that the rarity of sporangia and oogonia, the occurrence of vesicles on a few occasions only, and the non-pathogenicity of the isolate on potato tubers, place it near to *P. cambivora*. Its optimum temperature for growth is, however, much lower than that of *P. cambivora*. The identity of G_1 is therefore doubtful. Apart from pathogenicity on potato tubers, G_1 most closely resembles the isolates described above and identified as *P. Cinnamomi*.

H_1. The temperature range of isolate H_1 alone distinguishes it from all the other Cineraria isolates. It produced abundant and rapid growth from 20 to 32° C., but no growth at 35° C. Oogonia, sporangia and chlamydospores were not observed. The isolate was non-pathogenic on potato tubers.

Relating these features to Tucker's key (1931), the identity of this isolate might be *P. cambivora*, which is described briefly by Tucker as follows: 'Hyphae on agar media usually sterile. Vesicles occasionally developing, and oogonia rarely. Non-pathogenic on potato tubers. Optimum growth temperature is between 25 and 30° C. No growth occurred at 35° C.'

This description supports the probable identity of the isolate with *P. cambivora*.

H_1 formed no sexual bodies on transference from pea broth to sterile water. It was markedly intolerant of the most dilute solution of malachite green. Hence Leonian (1934) would group it as *P. cambivora*, *P. Colocasiae*, or *P. Porri*.

P. Porri ceases growth at a temperature below 31° C. H_1 continued growth when the temperature was reduced to 8° C. *P. Colocasiae* does not grow at so low a temperature. The papillate and pedicellate sporangia characteristic of *P. Colocasiae* were not observed. The identity of the isolate as *P. cambivora* is therefore confirmed. Thus there appears to be at least two well-defined species involved in the Root Rot of Cineraria:

P. Cinnamomi: isolates R_1, J_2, F_2.
P. cambivora: isolates H_1.

In addition, G_1 has not satisfactorily been classified under existing schemes.

The causal organism

Inoculation experiments have shown that symptoms of Root Rot of Cineraria were induced, within a few weeks, by the introduction into the surrounding soil of isolates R_1, J_2, F_2 and G_1. R_1, J_2 and F_2 have since all been identified as *P. Cinnamomi*. G_1 very closely resembles this species except for pathogenicity on potato tubers. The percentage successful infection induced by isolate H_1 was much lower. H_1 was identified as *P. cambivora*.

From the present study it would appear therefore that *P. Cinnamomi* is responsible in greatest measure for Root Rot in Cineraria. *P. cambivora*, though parasitic, is less virulent than *P. Cinnamomi*.

Summary

1. The symptoms of a Root Rot of Cineraria are described and a number of fungal isolations from diseased plants have been studied.

2. Considerable differences and variations were observed between these isolates, yet all apparently belonged to the genus *Phytophthora*.

3. Five isolates, from a variety of sources, were selected for more detailed experiments.

4. The isolates were cultured on several solid and liquid media, and their growth characters compared.

5. The influence of temperature, *p*H, and a range of concentrations of malachite green on the isolates has been studied.

6. Each Cineraria isolate was identified by its growth and response to various treatments, and finally, in spite of apparent considerable variation, most of the isolates were identified as *P. Cinnamomi*.

7. Inoculations of Cineraria plants showed that the three isolates identified as *P. Cinnamomi* were those which most rapidly produced symptoms of Root Rot. *P. cambivora* was a less virulent parasite.

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NEW AND INTERESTING PLANT DISEASES

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(With Plates VI and VII)

16.* Scale spotting of tulip bulbs

On 23 June 1941 Mr E. R. Wallace sent me some diseased specimens of tulip bulbs, variety Yellow Prince, that had been dug the day before from a fine, sandy soil near Spalding. The bulbs were of 12–14 cm. size and the outermost scale of each, though turning brown, was still somewhat fleshy and immature. Removal of this outer scale revealed brown markings on the first fleshy scale below. Many of the markings were pale, brown, indefinite, isolated spots a few millimetres across, which had coalesced where they were numerous to give irregular patterns on the surface of the scale. On some bulbs there were large, slightly sunken, rounded or heart-shaped areas with definite margins on the 'cheek' of the bulbs, and sometimes the whole of the tissues around the neck had a pale scalded appearance and stood out in marked contrast to the white portions of the scales. In a more advanced stage these areas had become patterned in light and dark brown rings and streaks (Pl. VI, fig. 1). The brown markings penetrated into the scale, but rarely, if ever, extended right through to its inner surface: on the other hand, similar but fewer markings were occasionally evident on the outer surface of the next inner scale. The trouble seemed to be restricted to the bulbs of plants that were still green or partially green, and was not noticed where the foliage had already died down completely.

The precise cause of this scale spotting has not yet been determined. Exactly similar symptoms were seen on tulip bulbs, also of the variety Yellow Prince, received from Lincolnshire in early July 1934. On that occasion the greater part of a stock lifted from a silt loam was affected. The bulbs had flowered well, but after lifting and before cleaning they were left in the open for a week in trays stacked ten to twelve in a pile. The period was one of hot sunshine and the top trays were unprotected, but these showed no more and no less of the trouble than the rest, and other adjacent varieties (Ibis and Brilliant Star) exposed in the same way were unaffected. Efforts to induce the condition in healthy bulbs by exposing them for a week to hot sun were unsuccessful. No fungus could be found in the spots, or be isolated from them, and although a bacterial organism, culturally very similar to *Bacillus coli* Migula, was isolated, infection experiments with it gave inconclusive results, and attempts to inoculate healthy bulbs with small pieces taken from affected ones were unsuccessful. One or two of the bulbs were sent to Dr E. van Slogteren, of the Laboratorium voor Bloembollenonderzoek at Lisse, who said he was familiar with the

* Previous contributions to this series were published in the *Transactions*, vols. XXII–XXVI.

trouble and regarded it as physiological in origin. He had already seen it that year in Holland on Yellow Prince and certain other varieties, and in his experience it was usually most severe in the best stocks and heaviest bulbs.

Attempts to isolate an organism from the bulbs received in 1941 also failed and the disease was not seen again until August 1944 when it was found on the variety Miss Blanche in Lincolnshire. It was then reported that the trouble occurs in that county to a greater or less extent each year in a number of varieties, is sometimes a source of very heavy loss, and is apt to be worse when the bulbs are lifted under wet conditions and are stored too thickly in warm, badly ventilated sheds.

17. Ring rot of green walnut fruits

On 20 September 1941 some green walnut fruits were brought to me which showed injury quite distinct from that caused by rooks. The fruits had fallen prematurely from two old, large trees growing in a private garden in Harpenden, and much of the fruit remaining on the tree was also clearly affected. Some fruits showed merely a small black, sunken area at the stigmatic end of the green husk, while in others the chief symptom was a relatively inconspicuous and roughly circular patch about an inch in diameter on one side of the husk immediately below the old stigmatic remains (Pl. VI, fig. 2). The tissues comprising this patch were uniformly raised above the level of the rest of the husk or were irregularly raised in a series of humps or corrugations: they were paler than the remainder of the husk and frequently showed a yellowish tinge. The boundary between the healthy and affected parts was marked by a wavy and often interrupted black band about two millimetres wide. Later, this blackened band broadened unequally and became a more or less complete ring; it also became sunken and showed a number of transverse cracks. Although the green portion within the ring projected well above the general level of the fruit at first, later it gradually became black and sunken and ultimately the green husk showed a uniformly black or blackish sunken patch, an inch or more across, on one side of the fruit. As the tissues blackened they became sprinkled over with orange-coloured sporodochia of a species of *Fusarium*. On a few fruits there was a patch on each side of the husk and occasionally the whole of the stigmatic end was involved.

The affected fruits were mostly immature and the shell within still relatively soft. On cutting through fruits still in the typical 'ring' stage, the tissues of the green husk around the remains of the stigma were found to be completely disorganized, as also were those in a narrow belt immediately below the black ring, whereas there appeared to be nothing abnormal about the tissues immediately below the green portion within the ring. The upper part of the shell below the remains of the stigma was yellow-brown and decayed for a distance of one centimetre or more from the tip, and was covered with a fine weft of cottony mycelium. The kernel itself appeared to be unaffected. In the later stages of attack the rot spread down the shell until the whole of it was brown and rotten. Before this

happens the central placental tissue becomes rotten. The kernel may remain healthy until the whole shell is decayed but sooner or later the skin covering it blackens and the flesh is reduced to a soft, yellow-brown mass.

Preliminary examination of the *Fusarium* occurring on the surface of the blackened fruits showed that the spores were predominantly 3–4-septate, with a range of dimensions of 23–33 × 3–4 μ for the 3-septate, and 30–39 × 4–5 μ for the 4-septate spores. Pure cultures were obtained from the sporodochia and the same fungus was isolated, though not consistently, from the decayed portion of the shell, but it was not possible to continue the observations at the time and the disease has not been encountered again. The specific identity of the *Fusarium* and its causal relation to the disease is therefore uncertain. Wollenweber (1931) has reported *F. lateritium* Fr. on walnut fruits in Germany and he considered it might well be parasitic on this host, as it is on a number of other fruit trees. He also mentioned that species of *Fusarium* had been reported on walnut fruits in France and Italy. Later, Wollenweber and Reinking (1935) listed three species—*F. lateritium* Fr., *F. sambucinum* Fuckel, and *F. avenaceum* (Fr.) Sacc.—as the cause of an uncommon fruit rot of walnuts. According to these authors *Fusarium* produces black spots at the flower end of the still green husks and penetrates, along with other fungi, into barren nuts: if the fruit stalks are implicated the fruits fall prematurely and keep badly.

18. Leaf spot of spinach (*Heterosporium variabile* Cooke)

In all probability this disease is much more widespread in Britain than the three existing records of it suggest. *Heterosporium variabile* was first recorded and named by Cooke (1877), who observed it on spinach leaves collected near Welshpool, and it was not reported again until Glasscock and Ware (1939) found it in May 1939 causing severe damage to 2½ acres of Prickly Seeded spinach sown the previous August in two plots in a market garden at Appledore, Kent. One plot sown in October and three others in the spring of 1939 were unaffected.

In May 1944 I received spinach leaves attacked by this fungus from Wimborne, Dorset. They represented two stages of a disease that had appeared about mid-April on a crop of the variety Nobel derived from imported seed sown early in September 1943. At first the appearance of the small white spots had suggested hail damage but on 23–24 April the trouble spread very rapidly over an acre of the crop. Spring-sown spinach of the same variety less than 100 yards away remained unaffected, and by mid-June three spring-sown crops of Nobel, in part from the same seed sample as that sown the previous autumn, had been cleared without showing signs of Leaf Spot.

Leaves in the early stages of attack showed small, sharply defined, rounded, white spots, 1–3 mm. across, scattered, but mostly on the upper half of the leaf, surrounded by a very narrow shrivelled or water-soaked band, and free from conidiophores and conidia of the *Heterosporium* (Pl. VII, fig. 3). In a more advanced attack there were many spots which were often coalescent, crowded towards the tip of the leaf, and covered or partly

covered with dark, olive-green or black spore tufts (Pl. VII, fig. 4). The leaves were turning brown and withering from the tips, and in the final stages some of them were almost covered with small, separate, dark fungus mats 1–3 mm. across. The fungus was at first mainly epiphyllous, then more or less equally abundant on both sides of the leaf.

19. *Botrytis* sclerotia in sainfoin seed

Mr C. C. Brett has informed me that on a number of occasions during recent years one or two of the seeds in certain sainfoin seed samples examined at the Official Seed Testing Station at Cambridge have developed black sclerotia during germination tests. Three such samples were met with in the early part of 1944 and Mr Brett kindly sent me several of the affected seeds. They were dead, with the contents mostly reduced to an amorphous mass. Little or nothing was left of the external parts except a skeleton network of the more resistant tissues, in which a number of black sclerotia were embedded. These sclerotia were individually about 3 mm. long, sausage-shaped, curved or irregular, depending partly on their position in the substratum. Each consisted of a very narrow, black rind, sometimes only a cell or two thick, surrounding a mass of interlacing hyphae. Plate cultures prepared from the sclerotia gave a scanty, but uniform, white to grey, aerial mycelium and a few erect conidiophores bearing whorls of conidia. Sclerotia varying in size and shape from rounded bodies 2–3 mm. across to elongated masses up to 1½ cm. long and ½ cm. wide, were produced in a ring near the edges of the plates: they were white at first but soon became black. The fungus was identified as a strain of *Botrytis cinerea* Fr.

20. *Phytophthora infestans* (Mont.) de Bary on *Lycium halimifolium* Miller

The following note is adapted from a memorandum kindly placed at my disposal by Dr G. H. Pethybridge, who prepared it in 1942 from observations made by him at the time.

Towards the end of the very wet August of that year Dr Pethybridge noticed that many of the leaves on the pendulous branches of a box thorn (*Lycium halimifolium* Miller) growing in a private garden at Bodmin (Cornwall) were brown and withered at the tips. Many also had one or more fairly large, roundish, brown spots on the lamina further back, sometimes reaching the margin and sometimes not. These leaves were being shed prematurely and readily fell off if touched. A large number of the abundant crop of bright red berries, and the calyx to which each was attached, were also affected. It was suspected that *Phytophthora infestans* (Mont.) de Bary might be the cause of the lesions, especially as potato Blight had been extremely prevalent in the neighbourhood. No fungus was visible on or around the lesions on the leaves still on the shrub, but when affected leaves were placed for twenty-four hours or so in a damp dish a copious halo of *P. infestans* grew out from the still green tissue surrounding the brown lesions, just as occurs with potato foliage spotted with

Blight. Moreover, this fungus was found surrounding the lesions on some of the damp fallen leaves and it was present also on some of the fruits.

No healthy, unsprayed potato foliage was available for cross inoculation purposes, but slices of healthy tubers were inoculated with spores from the *Lycium* leaves and berries, and suitably incubated at room temperatures. Within a day or two copious growth of *Phytophthora infestans* occurred on them, while uninoculated slices under the same conditions remained unaffected. An attempt to inoculate healthy *Lycium* leaves and berries with spores from blighted potato leaves gave inconclusive results: the leaves developed lesions similar to those on the growing shrub, but they soon became covered with mould growths and sporulating *Phytophthora infestans* could not be detected with certainty. The inoculated fruits did yield the fungus, but so did two out of three of the uninoculated controls. There was no reasonable doubt, however, that the attack on the shrub was due to spores from blighted potato foliage, which was abundant in the particular garden as well as in adjoining ones. The shrub concerned was growing in a position where temperature and atmospheric conditions must have been ideal for the attack.

The shrub affected was identified by Mr A. D. Cotton as *Lycium halimifolium* Miller (syn. *L. barbarum* Aiton non Linn., *L. vulgare* Dun., and *L. europaeum* Gouan non Linn.), which is said to be very closely allied to and scarcely specifically distinct from *L. chinense* Miller. *Phytophthora infestans* has been recorded from time to time on various Solanaceous hosts but only once before on *Lycium*. Vowinckel (1926) found it occurring naturally on *L. halimifolium* and succeeded in artificially infecting this species and *L. turcomanicum*. Although the present case, therefore, does not constitute a new host record for *Phytophthora infestans* it appears to be the first instance in which the potato Blight fungus has been reported on a species of *Lycium* in the British Isles.*

21. A seedling disease of celery caused by *Alternaria radicina* Meier, Drechsl. & Eddy

In April 1945 some diseased celery seedlings an inch or two high were received at the Plant Pathology Laboratory from a nursery at Eastrea in Cambridgeshire. They formed part of a large batch of seedlings raised from seed that had probably been derived from plants raised from imported seed. Another large batch of seedlings grown in the same soil but derived from a different source of seed was not affected. The diseased seedlings were examined by Dr Alex Smith, to whom I am indebted for permission to summarize his observations. He found that, although the seedlings presented all the symptoms of Root Rot caused by *Phoma apiicola* Kleb., there was no sign of the pycnidia of this fungus on them or on a sample of the seed from which the seedlings had been raised. He therefore made isolations from the material, and some of the affected seedlings, as well as several hundreds of the seeds, were placed on moist filter paper in Petri dishes and incubated for a few days at room temperatures. Pure cultures

* The record listed by Moore (1943, p. 12) is the one dealt with here.

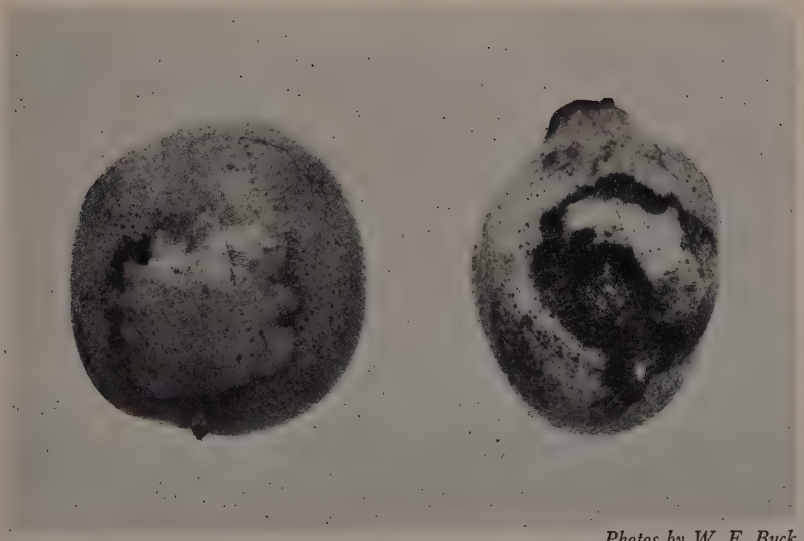
were obtained of a fungus which could not be distinguished from *Alternaria radicina* Meier, Drechsl. & Eddy, and the same fungus developed profusely on the affected seedlings and on practically all of the seeds incubated, as well as on celery debris mixed with the seeds. Pycnidia of *Septoria* appeared on a few of the seeds but *Phoma apiicola* was not seen. A few of the less badly affected seedlings produced a number of healthy rootlets in the Petri dishes, and the nurseryman reported that affected seedlings often made fresh roots and recovered from the disease after they had been pricked out.

Alternaria radicina has been known abroad since 1918 as the cause of a Black Rot of carrots, and in recent years it has been found on several occasions attacking carrots in this country (Moore, 1943, p. 44). As far as I am aware, however, it has not previously been reported on celery, although Neergaard (1935, 1936, 1937) has described it as the cause of damping-off of celeriac seedlings in Denmark and of a black mould scab (Selleriens Sortskimmelskurv) of celeriac tubers, on which it forms a dry, brown, cracked crust a few millimetres thick. Neergaard proved that the fungus was pathogenic to the roots, tubers, stems, petioles, leaves, umbels and seeds of celeriac and demonstrated that it could be both soil and seed transmitted. He also found the fungus attacking parsnip roots and parsley in Denmark.

22. Snow rot of wheat (*Typhula graminum* Karst.)

In certain parts of Europe, notably Scandinavia and northern Germany, and in the United States of America and Japan, considerable rotting and yellowing is frequently revealed in winter crops of wheat, barley, and rye when the snow melts in spring. The young plants are backward in growth, the leaves become yellow and brown from the tips downwards, and many plants may be killed outright. Others survive, slowly grow away from the disease, and may produce weak and badly filled heads. The rot is usually attributed to the sclerotium-forming fungus *Typhula graminum* Karst. but, as Remsburg and Hungerford (1933) have indicated, there are probably a number of different species of the form genus *Sclerotium* which attack cereals and grasses. One of them, *S. rhizodes* Auersw., was recorded in England on grasses some years ago (Stirrup, 1932) and another, which corresponded closely to the description of *Typhula graminum* Karst. in its sclerotial state, was found on wheat at Leverstock Green, Herts, in February 1945. Shortly after a heavy fall of snow small patches of the young plants on the headlands of a large field of wheat attracted attention because the outer leaves had begun to turn yellow and wither. When Dr Alex Smith examined some of the plants in the laboratory he found a few small, brown or greyish-brown sclerotia, about the size of a pin's head, on the crowns and the withered leaf sheaths. The symptoms and sclerotia recalled the *Typhula* disease described and illustrated, for instance, by Volk (1937). Only a little material was available and when the field was revisited towards the end of March the wheat was growing vigorously, and, apart from a certain amount of wireworm damage, appeared to be healthy. It was only after careful search in the particular part of the headlands where the patches had been seen, that two or three plants bearing sclerotia

Fig. 1.



Photos by W. F. Buck

Fig. 2.

Photos by W. F. Buck

Fig. 4.

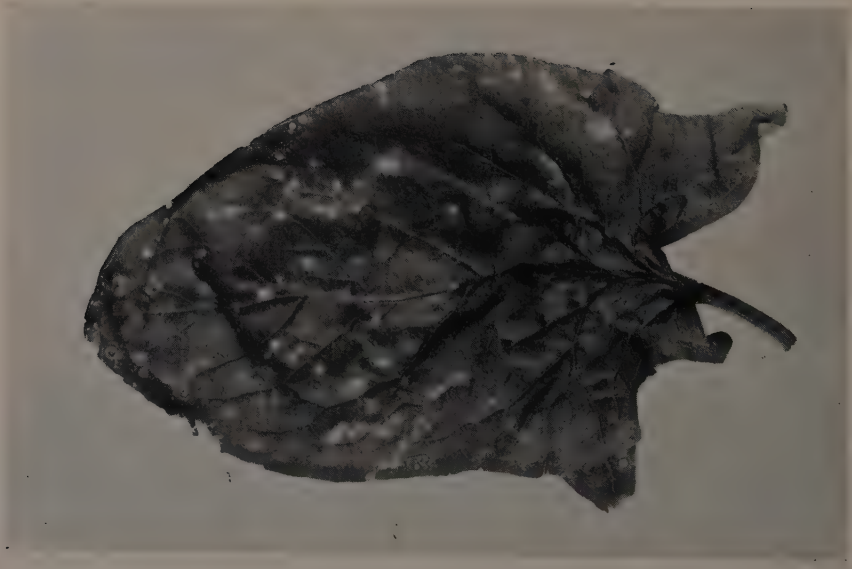


Fig. 3.

could be found. They were present on the oldest withered leaf sheaths, and beyond the fact that they were somewhat dwarfed, the plants appeared to be healthy. Pure cultures were obtained from the sclerotia, and though no sporing stage was observed on the plants or in culture, there is little doubt that the fungus concerned was the one commonly called *T. graminum* Karst. According to Imai (1936), however, it is really distinct from that species and might properly be called *T. itoeana* Imai. In tubes of dextrose agar the fungus produced only a very scanty aerial mycelium and soon began to form one or more coralloid masses of sclerotia on the surface of the agar slope. These masses, which were a few millimetres to over a centimetre across, and projected up to $\frac{1}{2}$ cm. above the agar slope, were honey coloured or pinkish at first, but soon became reddish brown with a rather glistening appearance. In section they consisted of a mass of interlacing, colourless hyphae surrounded by a very narrow but clearly defined, reddish brown rind.

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EXPLANATION OF PLATES VI AND VII

Plate VI

Fig. 1. Tulip bulbs showing scale spotting of uncertain origin.

Fig. 2. Green walnut fruits with ring rot. The one on the right bears sporodochia of *Fusarium* sp.

Plate VII

Fig. 3. Spinach leaf illustrating early stage of attack by *Heterosporium variabile* Cooke.

Fig. 4. A later stage with *Heterosporium* developing on the spots.

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PHYSIOLOGIC RACES OF THE CROWN GALL ORGANISM IN BRITAIN

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(With Plates VIII and IX)

The discovery by Smith and Townsend (1907), that crown gall of plants is caused by a bacterium, stimulated research on various aspects of this disease in many countries. Since 1907 hundreds of papers on crown gall have been published, many of them in the United States, particularly by Erwin F. Smith and his school, and by Riker and his collaborators who have given special attention to galls, hairy root, and wound overgrowths of nursery fruit trees (see, for example, Riker & Keitt, 1925, 1926; and Riker & Muncie, 1926). On the Continent, too, many papers have appeared including several dealing chiefly with crown gall on nursery trees, e.g. Stapp (1938), Stapp *et al.* (1938).

In Britain, crown gall has received comparatively little attention, particularly experimentally. Massee (1910*a*, *b*), in early accounts of its occurrence in this country, at first followed Toumey (1900) in attributing the disease to a myxomycete, *Dendrophagus globosus* Toumey, but later (1915) accepted the findings of Smith and Townsend. An anonymous note in the *Journal of the Ministry of Agriculture* in 1911 describes root tumours on sugar beet that were probably crown galls. In 1921 Walkden announced the isolation of *Bacterium tumefaciens* E. F. Sm. & Towns. from a crown gall on Paris daisy (the garden marguerite *Chrysanthemum frutescens*), and was the first to show that the crown-gall organism was actually present in Britain; later Robinson and Walkden (1923) published results of further work on the disease. Ramsbottom (1927) briefly discussed the analogies between plant crown galls and human cancer, with special reference to a paper by Robinson (1927). Berridge (1929, 1930) studied *Bacterium tumefaciens* in relation to the *p*H of cell sap. Butler discussed the anatomy of crown gall in two papers (1930, 1931), the latter one criticizing the emphasis that some workers placed on the analogies between crown galls and animal tumours (including human cancers). The plant disease known as leafy gall, but caused by a different organism, *Corynebacterium fascians* (Tilf.) Dowson, has been investigated in England by Williams (1933–5), and by Lacey (1936*a*, *b*, 1939, 1942).

About the year 1920, crown gall began to be studied at the East Malling Research Station because of its frequent occurrence on apple and pear varieties raised vegetatively (by layering or stooling) for rootstocks. A brief account of trials for its control in the nursery was given by Wormald and Grubb (1922), who later (1924) described field observations with particular reference to the relative susceptibility of the rootstock varieties. When it was found that crown gall caused little or no damage to either apple rootstocks in the nursery or to orchard trees, investigations on an intensive

scale were discontinued, though observations and experiments were made from time to time; Hatton, Wormald and Witt (1926, 1928) described burr-knots in relation to their supposed resemblance to crown gall; Harris (1931) made experimental studies of the relative susceptibility of apple rootstock varieties, and this work was carried a step further by Harris and Pearse (1938) who also induced galls on apple stocks by using a growth-promoting substance. Wormald and Garner (1945) describe an experiment in which an organic mercurial preparation gave noticeable control of crown gall on vegetatively raised apple stocks.

The evidence as to whether crown gall is really detrimental, particularly to apple rootstocks and the trees worked on them, is contradictory. Certain American workers maintain that the galls do have an adverse effect. Fracker (1918*a*, *b*) found that more non-infected trees could be classed as grade I than those bearing galls or hairy root, and Greene and Melhus (1919) write: 'The data presented show that crown gall greatly retards the growth activities of young apple trees. It is followed by a reduction in the amount of increase in trunk diameter, and in the number of twigs, their length, their thickness, and their weight.'

It has been observed at East Malling that, on some batches of comparable trees, the largest galls were on the most vigorous trees, and Russian observers have stated that trees with crown gall are sometimes more vigorous than those free from galls (see Jaczewski, 1935, p. 482). Harris and Pearse (1938) obtained evidence that 'inoculations with *B. tumefaciens* had a measurable stimulating effect on the growth of the host trees'.

Apple trees on vegetatively raised rootstocks planted out at East Malling, some with galls others without, showed no difference in vigour or cropping for eighteen years. It is to be noted, however, that apple rootstocks raised from layers or stools do not become infected until after they have been removed from the 'parent' layer or stool and planted out in the nursery. Seedling apple trees, on the other hand, may develop galls at the collar in their first year (Pl. VIII, fig. 3) and two-year-old seedling apple trees have been seen with galls weighing about 40 % of the total weight of the trees (Wormald & Grubb, 1924): the effect of such large galls relative to the trees bearing them has not been tested.

The galls are sometimes enormous in comparison with the organs bearing them. Apple roots only about 2 mm. in diameter have been found with galls 5–7 cm. across. Such galls must absorb large quantities of nutrients that might have been utilized by the plant for building up normal healthy tissues.

Evidence that crown gall may sometimes be definitely harmful has been seen on pear layers and on raspberry stools where buds have developed into galls instead of into shoots, and on cultivated blackberries where buds on the canes are transformed into galls that sometimes cause the canes to split into strips.

The host plants of crown gall are many; Jaczewski (1935, p. 458) listed 66 species of plants (of thirty-nine different families) on which crown gall had been recorded or had been induced by inoculation up to 1931, and since that time the number has increased considerably.

In connexion with the occurrence of the disease at East Malling the writer collected tumours (from their general appearance and absence of any obvious parasite apparently of the crown gall type) from apple (layered stocks and seedling trees), pear (layered stocks and stools), *Pyrus Toringa* (crown), hawthorn (stools), peach (root), plum (root), loganberry (roots), cultivated blackberry (canes), rose (particularly Manetti root-stocks), hop (crown), beetroot (crown), mangold (crown), melon (leaves), *Scolymus* (crown), dahlia (crown), phlox (stems), hollyhock (crown), *Schizanthus* (crown), runner bean (crown), dock (crown), *Chaerophyllum bulbosum* (crown), *Eucalyptus* sp. (on crown of seedling plant), and lupin (crown). Other plants on which crown gall was found in England during the period 1933–42 (Moore, 1943) are swede, sugar beet, tomato, vegetable marrow, Japanese quince (*Cydonia japonica*, on imported plants), gooseberry (twigs), youngberry, *Asparagus Sprengeri*, and chrysanthemum. The hosts of crown gall recorded for Scotland (Dennis & Foister, 1942) are sugar beet, mangold, tomato, raspberry, *Chrysanthemum indicum*, sweet pea, and *Potentilla* sp. (Gibson's Scarlet).

It is not certain that all the galls examined or recorded were true crown gall caused by *Bacterium tumefaciens*, as superficial examination is not enough for diagnosis, and the isolation of a gall-inducing bacterium having certain cultural characters is the only reliable criterion. Up to the present, Walkden's paper is the only published account of the isolation of a gall-producing bacterium from crown galls (excluding 'leafy galls') found in Britain, though it has been briefly stated that strains of *B. tumefaciens* have been isolated at East Malling (*Rep. E. Malling Res. Sta.* for 1939, p. 28, and 1940, p. 23). It is assumed, however, that *B. tumefaciens* is the cause of these crown galls in Britain (see Moore, 1943, and *Advisory Leaflet*, no. 253, of the Ministry of Agriculture), the assumption being based on the analogy they bear to galls, that have been shown by isolation and inoculation experiments to contain *B. tumefaciens*, on host plants in America and on the Continent. It is to be noted that much of the earlier experimental work in Europe was made with cultures distributed by E. F. Smith, but more recently Stapp and his colleagues in Germany have obtained isolates of *B. tumefaciens* from galls on a number of hosts.

Isolates were obtained from many of the galls I examined, and some of the organisms have proved to be able to induce galls when inoculated into certain plants. Others have given no evidence that they are pathogenic; whether these were 'avirulent' strains of *B. tumefaciens* or quite different organisms was not determined. As the work proceeded it became evident that the pathogenic strains were not identical, and certain differences among them, particularly with regard to their host relationship, are here described.

Isolation

Because of the relatively few bacteria in galled tissues the isolation of the causal organism offers special difficulties, and some workers have had recourse to original methods or special culture media. The method I have generally employed is as follows:

The gall is scrubbed with a hard toothbrush in a stream of tap water and the surface then dried with filter paper. A small piece of the gall is broken off and (impaled on a needle) flooded with a drop of absolute alcohol which is immediately burnt off; a clean surface is cut with a sterile scalpel and a small bit of clean-looking tissue is removed on the point of the scalpel and placed in a sterile petri dish, where it is crushed with the end of a sterile glass rod and then transferred to a tube of carrot extract. Several tubes are prepared in this way and incubated (25° C.). When any tube shows characteristic growth isolation plates of carrot agar are prepared. The features looked for in these preliminary tubes are, slow growth (the liquid becoming slightly turbid only after several days), followed by the formation of a thick, white, somewhat gelatinous pellicle, without any pronounced turbidity of the liquid. The plate colonies are raised, shiny, translucent, with a dense, white centre.

Carrot extract has been found to be a useful culture medium, for the crown gall organism grows well in it and (with transfers every six months) retains its virulence for years without reisolation from a host plant.Thus one of the strains used is that isolated in 1919 by Walkden, who kindly sent me a subculture soon after he described his isolate (Walkden, 1921); it has been grown in carrot extract ever since, and when recently (1943) tested for pathogenicity it produced galls 2–3·5 cm. in diameter on Paris daisy—more than twenty years after its isolation.

Carrot extract agar has been used for the isolation plates, and for streak cultures, in tubes or in plates, for plant inoculations.

The first isolates obtained at East Malling were from a number of apple galls, from a specimen showing hairy root, and from a pear rootstock, but they gave no very conclusive results when inoculated into young apple trees or into stems of tomato, raspberry, *Chrysanthemum coronarium* or *C. frutescens*, although certain apple isolates when inoculated into young apple stems did cause the development of small galls (see Pl. IX, figs. 8, 9), the largest measuring $14 \times 8 \times 7$ mm. and $13 \times 12 \times 8$ mm., and from two of them the organism was reisolated. Patel (1927), and Stapp *et al.* (1938) found that isolates from apple galls are often avirulent, and Brown and Leonard (1932) refer to the frequent occurrence of non-virulent colonies of *Bacterium tumefaciens* on plates made from known crown gall tissue.

On the other hand isolates from other hosts will readily infect apple, and at East Malling large galls have been induced on apple by inoculations with strains from raspberry and from dock (Pl. IX, fig. 10). Walkden's strain, though very virulent on Paris daisy, when inoculated into apple has produced only one small gall from twenty-five inoculations.

Inoculation experiments

During the period 1920–33 many inoculations were made and the results are summarized in Table 1. Some of the strains used were obtained from other workers and their source is given. The general result, usually of a number of experiments, is indicated by ++ (well-developed galls), + (small galls), ? (slight swelling, doubtfully gall tissue, possibly wound-callus), 0 (no outgrowth).

Table 1. *Summary of results of inoculations with isolates of* Bacterium tumefaciens, 1920–33

Origin of isolates	Inoculated host plants: Apple	*Chrysanthemum frutescens*	*C. coronarium*	*C. sinense*	Raspberry	Tomato
Apple	+, ?, or o	o	o	—	—	o
Apple (Riker)	—	o	—	—	—	++
Bramble	o	—	—	—	—	—
Daisy (Walkden)	+ or o	++	—	+	+	+
Daisy (E. F. Smith)	—	++	—	—	—	—
Dock	++	o	—	o	++	++
Dock R	—	o	—	—	—	—
Hollyhock	—	—	o	—	—	+
Hop (E. F. Smith)	—	—	++	—	—	++
Poplar (E. F. Smith)	—	—	++	—	—	++
Raspberry 1	++	o	o	o	++	++
Raspberry 2	++	+ or o*	—	?	++	—
Raspberry R	—	o	—	—	—	—
Raspberry (wild)	o	—	—	—	—	—
Raspberry (Riker)	—	o	—	—	—	++
Schizanthus	—	o	—	—	—	?

* Three out of ten inoculations yielded small galls.

The inoculations on Paris daisy and on tomato were, as a rule, well marked; with any one strain the inoculations usually gave either all positive results (with well-developed galls) or all negative (with no trace of galls). On apple, however, with strains virulent for that host some only (25–50 %) of the inoculations were successful, resulting in large galls, the others giving no abnormal growth whatever. Thus in one experiment, using raspberry, dock and daisy (Walkden) strains, each inoculated into sixteen trees, four inoculated with raspberry and five with dock strains yielded large galls, one with daisy strain a small gall, and all the rest (including sixteen inoculated with an apple isolate) gave no abnormal response. In another experiment with raspberry strain on twenty-four apple trees all of the same age and variety, thirteen trees developed large galls, the rest no trace of galls. Similar erratic results have occurred in other experiments on apples, and at present the cause is unknown. Harris and Pearse (1938) have indicated the possibility, however, that the organism may have an appreciable effect on the tree in the absence of a gall, so that failure to produce a gall cannot be accepted as absolute proof of a negative result of inoculation.

That there are races of *B. tumefaciens* which are pathogenic on some hosts and not on others has been established by workers abroad, e.g. Smith, Brown and Townsend (1911), Siegler (1928), Stapp *et al.* (1938), Dame (1938). On the other hand, Kapshuk (1933), in Russia, made several isolations from various hosts and from the soil of infected orchards and found that they were identical in morphological and cultural characters and were equally virulent on beet, tobacco, and tomato.

As shown above certain strains of *B. tumefaciens* readily induced galls on Paris daisy, while others failed on daisy but infected tomato. As this indicated some degree of physiologic specialization, confirmation was deemed necessary. The inoculation experiments, discontinued in 1933,

were therefore resumed in 1939, when some of the strains of previous experiments, and others more recently isolated, were used on Paris daisy and tomato. The results are shown in Table 2.

All the strains used had been isolated by myself except Walkden's daisy strain. The fraction shows the number of inoculations (denominator) and the number yielding galls (numerator). The inoculations were made by placing bacterial slime (from a stroke culture on carrot agar) on the stem and making a puncture through it into the stem, with a sterile needle. The figures in brackets are not strictly comparable with the rest; they show the mean size of the galls that developed, ignoring the inoculations that failed. The Paris daisy plants were from a clone propagated by cuttings; the tomato plants were seedlings of one variety.

Table 2. *Results of inoculations on Paris daisy and tomato*

Strain of *B. tumefaciens*	Paris daisy		Tomato	
	Result	Mean diam. of galls in mm.	Result	Mean diam. of galls in mm.
Daisy	8/8	20·7	6/6	6·3
Dock R*	0/6	—	4/4	15·5
Raspberry R†	0/5	—	4/4	11·0
Bramble	0/4	—	2/6	(2·5)
Blackberry‡	0/4	—	6/6	2·3
Loganberry 1	0/4	—	4/6	(3·2)
Loganberry 2	0/5	—	6/6	10·6
Hollyhock	0/3	—	6/6	7·3
Runner Bean	0/4	—	3/6	(3·3)
Schizanthus	0/4	—	2/4	(3·0)
Control	0/6	—	0/4	—

* Originally from dock but reisolated from tomato.
† Originally from raspberry but reisolated from tomato.
‡ From a cane gall of the cultivated variety Black Diamond.

The table shows that (1) on daisy, only the daisy isolate produced galls, (2) on tomato all produced galls but in various degrees, (3) the largest galls on tomato were induced by isolates dock R, raspberry R, and loganberry 2, those of the daisy strain being only of medium size, (4) one loganberry strain was far more virulent than the other on tomato, (5) an isolate, originally from a weed (dock), and one from a hedgerow plant (bramble) induced galls on tomato, that from dock being particularly virulent.

At each point of inoculation on daisy with the daisy strain, the gall had a double structure; a gall arose at the point of inoculation and another on the opposite side of the stem; these two eventually met so that the stem became girdled.* From each of two inoculations, in addition to the ordinary rounded galls, an elongated gall developed on a petiole immediately above the point of inoculation, on one of them extending along the midrib of the lamina nearly to the apex. Such secondary galls on leaves have been observed by Smith *et al.* (1912), and by Robinson and Walkden (1923).

On the tomato stems a large gall was usually accompanied, on the side opposite the puncture, by a smaller and smoother secondary gall, as in

* In the table each double gall is counted as one.

daisy. On some again there were pimple-like swellings between and around the galls; they were smooth, circular, mostly 2–3 mm. in diameter, and they appeared on all plants inoculated with isolates dock R, raspberry R and loganberry 2, and on one with hollyhock. These small outgrowths appear to be the 'extruding secondary tumors' described by Suit and Eardley (1935).

The original dock isolate was obtained from a gall at the crown of a plant of *Rumex crispus* growing as a weed on the East Malling Research Station. That crown gall occurs on wild plants and weeds is of some significance, since such plants may serve as unsuspected hosts of *Bacterium tumefaciens*. Other workers record its occurrence on *Rumex crispus* (Muncie, 1930), *Rumex acetosella* (Palm, 1934), and *Malva rotundifolia* (Hildebrand & Massey, 1942).

In 1940 similar series of inoculations were made on Paris daisy and tomato, and the original isolates from dock and raspberry were also included. The results were comparable with and confirm those of 1939. Again only the daisy strain infected daisy, with galls 3–5 cm. in diameter. On tomato the largest galls were induced by the original dock and raspberry isolates, those next in size (but only slightly smaller) by dock R, raspberry R, and loganberry 2; the daisy strain again produced rather small galls, and in this experiment isolate loganberry 1 produced no galls.

The results on *Chrysanthemum frutescens* and *C. sinense* suggested that the daisy strain might have some physiological adaptation to plants of the family Compositae, and this was supported by inoculations on stems of the scentless mayweed (*Matricaria inodora*) growing as a weed on the Station, using daisy and dock R strains; the daisy strain produced galls 4–9 mm. in diameter, while no galls appeared on those stems inoculated with dock R, or on control stems. Other plants of the family have not been tested.

In 1941 further experiments were made to test the virulence of certain isolates; the chief points of interest arising from the results were these:

(1) Two fresh isolates had been obtained from raspberry galls in 1940, one from a typical crown gall at the base of a cane, the other from a gall on the upper side of a rhizome; the latter had apparently grown from a bud which had developed into a gall instead of into a normal cane. When inoculated on tomato both isolates produced galls up to 4 cm. in diameter but they were non-virulent on Paris daisy, while Walkden's strain tested on daisy at the same time produced galls 2–4 cm. in diameter. These and previous results showed that three separate isolates from raspberry infected tomato but not Paris daisy; one other produced a few small galls on daisy (raspberry 2, see p. 138).

(2) The original raspberry isolate was a typical smooth type for some years (it was isolated in 1926), but about 1937 it had become 'rough', and stroke cultures on agar were furrowed, dull, and of feeble growth. It was thought that it might have lost its virulence, but when inoculated into tomato stems, through punctures and on the exposed surfaces of cut ends of stems, galls 1·5 cm. in diameter developed at the punctures, and 2 cm. at the cut ends.

(3) The isolate raspberry R (reisolated from tomato in 1927) had been

inoculated into apple stems in 1939, and large galls were present on some of the trees in the winter 1940–1. Isolates, which appeared to be *Bacterium tumefaciens* were obtained from two of these galls, and one of them was inoculated into tomato stems; only very small outgrowths, possibly incipient galls, appeared at some of the punctures. This result suggests that the organism, in passing through apple, had almost lost its virulence. As already mentioned many isolates from galls arising naturally on apple are non-virulent.

In 1942 inoculations with strains isolated from *Rubus* spp. were made on raspberry canes grown in pots in a greenhouse with the results shown in Table 3.

Table 3. *Isolates from* Rubus *spp. inoculated into raspberry canes*

Source of strain	Result	Mean size of galls in mm.
Blackberry (cultivated)	4/12	(2·2)
Bramble	8/12	(2·1)
Loganberry 1	3/12	(2·0)
Loganberry 2	12/12	9·2
Raspberry (crown, 1940)	12/12	8·0
Raspberry (rhizome, 1940)	12/12	9·5
Control	0/15	—

The results are comparable with those on tomato, and show the marked virulence on raspberry of isolates from raspberry and of loganberry 2. The two loganberry isolates were from material (roots) obtained from widely separated places, and they appear, from their different virulence and behaviour in culture (see p. 143) to be different strains.

Culture tests

Although complete cultural examination of the strains used in the inoculation experiments has not been made, the tests applied have shown that the organisms have affinity with certain named strains (Walkden's daisy, and isolates from E. F. Smith and A. J. Riker). The apple and pear strains show these characters in common with named strains:

(1) Gelatin is not liquefied.

(2) Growth is strictly aerobic; there is no growth in the closed arm of fermentation tubes.

(3) Growth in liquid media is almost entirely at or near the upper surface, where a firm pellicle is formed. This pellicle in vegetable extracts is a character common to all strains; in carrot extract, with some isolates it attains a thickness of about 1 cm.

(4) The colonies on carrot agar plates, and the streak cultures, are smooth and glistening, somewhat hyaline but with a dense, more opaque, white centre.

(5) On sterilized potato there is a white, spreading, glistening growth.

In some characters they diverge somewhat from the named strains. The growth in sugar-containing media is very similar but they give a more acid reaction. This production of acid is well shown in milk cultures; with

the apple and pear isolates an acid curd is produced, with the named isolates a soft curd with no acid. In litmus milk there is reduction of the litmus, and the acid reaction is more clearly shown by 'purple milk' (bromo-cresol-purple as indicator) in which the East Malling apple and pear isolates turn the medium yellow, most of the named strains bluish purple. In purple lactose agar the same acid reaction is shown. This production of acid they have in common with Dr Riker's raspberry strain, which however does not show it so markedly as the East Malling apple and pear isolates; this raspberry strain is probably the isolate described by Riker (1923) as turning litmus milk pink.

When it was found that some isolates showed marked virulence on tomato, apple, and raspberry, but not on daisy, cultural tests were made for comparing them with the daisy strain, to ascertain if there was any correlation between cultural reaction and degree of virulence in relation to host plants.

The ten isolates of Table 3 together with the original dock and raspberry isolates were tested on purple lactose agar and indicator milk, for these media had already shown the divergence of the apple isolates from type strains.

On purple lactose (1 %) agar (slope cultures) all gave a slight alkaline reaction within twenty-four hours. Isolates loganberry 1, runner bean, and *Schizanthus* remained alkaline, the rest showed, sooner or later, some acidity, the reaction starting at the upper end of the slope. In isolates dock, dock R, raspberry, raspberry R, bramble and loganberry 2 this acid reaction started on the second day after inoculation and was more pronounced than in the other isolates. It became reversed, however, and after three weeks all again showed an alkaline reaction, which persisted to the end of the experiment (three months).

On purple lactose (2 %) agar the reaction was again alkaline within twenty-four hours, but afterwards the acid reaction was more pronounced than with 1 % lactose. Isolates dock, dock R, raspberry, raspberry R, and loganberry 2 showed marked acidity (the medium turning bright yellow throughout) within four to six days, the bramble isolate a little later; this marked acidity persisted (three months). The *Schizanthus* isolate remained alkaline throughout the experiment. The daisy, loganberry 1, bean, blackberry, and hollyhock isolates, after the initial change to alkalinity, gave a slight acid reaction which persisted in the first three, but in the other two reverted to alkalinity.

These results show that the strains most virulent on tomato are those that produce acid most readily from lactose. The bramble strain (feebly parasitic on tomato) also gave an acid reaction on purple lactose agar, but this strain in carrot extract produces more turbidity and a thinner pellicle than the rest, with a tendency to form bubbles of gas at the surface; probably therefore it should not strictly be included under *Bacterium tumefaciens*.

The milk media were (1) plain milk (without indicator), (2) litmus milk, (3) methylene-blue milk, (4) purple milk.

The results as regards curdling of the casein was (as expected) approxi-

mately the same for any one isolate in all four media, the only differences being those of colour due to the indicators.

As the litmus was reduced by all the isolates it proved unsuitable for showing change of reaction.

The methylene blue was reduced by all within four days, but later colour returned in those tubes, which, as shown by the purple milk, were definitely acid.

The indicator of the purple milk was not reduced and so served to show clearly any change in reaction. Within the first four days after inoculation all showed a reaction in the alkaline direction. Later, however, some of the isolates showed a distinct acid reaction, accompanied by curdling of the casein. After five weeks the results were as shown below.

Table 4. *Reaction in purple milk of various isolates after five weeks*

Isolate	Action on casein	Colour of medium	*p*H
Daisy	No curd	Blue purple	7·0
Dock R	Solid curd	Yellow	5·4
Raspberry R	,, ,,	,,	5·4
Bramble	Soft curd with a little whey	Slightly bluer than control	6·3
Blackberry	Slight separation of curd above	Blue purple	7·0
Loganberry 1	,, ,, ,, ,,	Bluer than control	6·6
Loganberry 2	Solid curd	Yellow	5·7
Hollyhock	No curd	Blue purple	7·0
Runner Bean	Slight separation of curd above	Bluer than control	6·5
Schizanthus	,, ,, ,, ,,	,, ,, ,,	6·5
Dock (orig.)	Solid curd	Yellow	5·4
Raspberry (orig.)	,, ,,	,,	5·4
Control	No curd	Purple	6·2

The most striking results from these cultural experiments is that strains non-virulent on chrysanthemum yet most virulent on tomato and apple produced a definite acid reaction (as shown by the final *p*H of the media) in milk and in lactose agar, media containing lactose. What bearing, if any, this has on the relation between these parasites and their hosts has not been investigated.

The general conclusion to be drawn from the inoculations and cultural tests is that within the species *Bacterium tumefaciens* there are, in Britain, physiologic races with different host relationships and habit in cultures.

Four categories can be distinguished:

(1) The daisy (chrysanthemum) type (apparently similar to the original *Bacterium tumefaciens* E. F. Sm. & Towns.) which readily infects Paris daisy; it produces galls of medium size on tomato and raspberry, rarely on apple. This type shows no definite acid action in media containing lactose.

(2) The dock type (including raspberry and probably loganberry 2 isolates) does not infect Paris daisy but produces large galls on tomato, apple, and raspberry. It gives a marked acid reaction in lactose media (an acid curd in milk).

(3) Other isolates do not infect Paris daisy, but induce small galls on tomato; they mostly produce a little acid in purple lactose agar but not in milk.

(4) Isolates from apple and pear have produced either only small galls

or no galls at all on apple stems, and negative results on other hosts inoculated. They develop acid in media containing sugar (sucrose, dextrose, or lactose), and an acid curd in milk cultures.

Summary

Previous descriptions and work on crown gall in Britain are reviewed.

Investigations on crown gall at the East Malling Research Station were started in connexion with its occurrence on apple rootstocks, but gall-inducing isolates were obtained from a number of other hosts for comparison.

The organisms examined showed differences in their host relations and reactions in culture, and four categories can be distinguished.

Of two of the organisms isolated one was from a common weed (curled dock) and the other from a hedgerow plant (bramble).

For cultures of *Bacterium tumefaciens* isolated by other workers I am indebted to the late Dr Erwin F. Smith, to Dr A. J. Riker, and to Mr H. Walkden. I thank also Mr R. V. Harris for his interest and help throughout the investigation and for helpful criticism of the script of this paper.

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EXPLANATION OF PLATES VIII AND IX

Plate VIII. Natural infections

Fig. 1. Crown gall on dock (*Rumex crispus*).
Fig. 2. Crown gall on raspberry.
Fig. 3. Galls on seedling apple trees.
Fig. 4. Basal, lateral and root galls on an apple rootstock.

Plate IX. Galls induced by inoculating with pure cultures of *Bacterium tumefaciens*

Fig. 5. Tomato stem inoculated with isolate from dock.
Fig. 6. Tomato stem inoculated with isolate from loganberry.
Fig. 7. Tomato stem inoculated with isolate from daisy (*Chrysanthemum frutescens*).
Figs. 8, 9. Apple stems inoculated with isolates from apple.
Fig. 10. Apple stem inoculated with isolate from dock.

All reduced to $\frac{3}{4}$ natural size.

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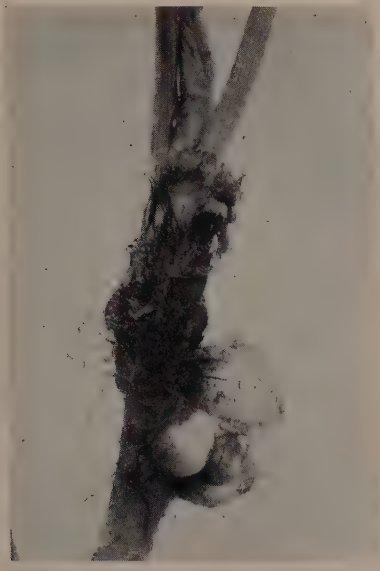

Fig. 1.

Fig. 2.

Fig. 3.

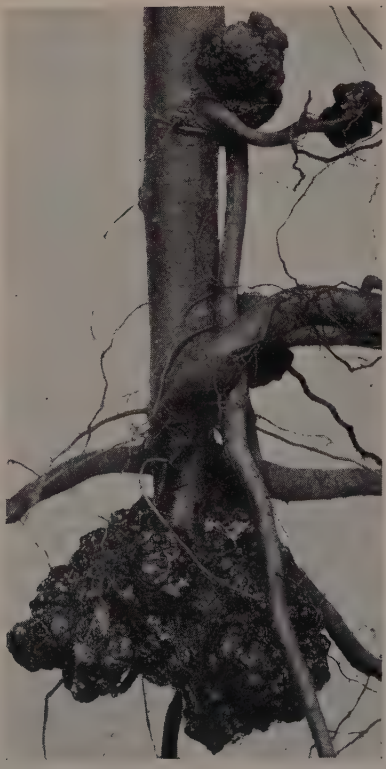

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

Fig. 9.

Fig. 10.

PLANT PATHOLOGY MEETING, EAST MALLING

20–21 July 1945

The Nineteenth Annual Plant Pathology Field Day and the annual phytopathological meeting were combined as a two-day meeting which was held at the East Malling Research Station, by courtesy of the Director, on 20 and 21 July 1945.

A party of approximately fifty members and friends was officially welcomed by the Director, Dr R. G. Hatton, C.B.E., F.R.S., at Bradbourne House, after which short talks were given by Messrs R. V. Harris, H. Wormald, H. B. S. Montgomery, and M. H. Moore on special problems under investigation at the Station. Lunch was taken at Bradbourne, following which a tour was made of the plantations, and demonstrations were given on Shoot Wilt of Plum Layers (*Cylindrocladium* sp.) by Dr Wormald, Bacterial Canker of Stone Fruits (*Pseudomonas mors-prunorum*) and Apple Canker (*Nectria galligena*) by Mr M. H. Moore, Control of Raspberry Cane Spot (*Elsinoe veneta*) by Dr R. V. Harris, and the recording of Apple Scab (*Venturia inaequalis*) on foliage by Miss M. Bennett. After tea a very interesting series of laboratory exhibits was inspected including the Laboratory Testing of Fungicides by Dr H. Shaw and Miss M. P. English, Species and Strains of *Verticillium* by Mr I. Isaac, Shoot Wilt of Plum Layers and Strawberry Leaf Blotch by Dr Wormald, *Verticillium* Wilt of Hops by Dr W. G. Keyworth, and Virus diseases of Fruit by Mr I. W. Prentice.

The second day was spent mainly on hop problems, and introductory talks were given by Messrs Harris, Keyworth and Isaac. Another tour of the experimental plots followed before returning to an excellent lunch kindly provided by the Station. The afternoon was devoted to visiting hop gardens in the Paddock Wood area, where examples of both 'fluctuating' and 'progressive' types of *Verticillium* outbreaks were inspected. Tea was taken after returning to the Station and the gathering dispersed at 5 p.m.

The meeting was voted a great success by all present, and the credit for this is due entirely to the hard work of the East Malling staff who were responsible for all the arrangements. The meeting expressed its appreciation and thanks to the Director and staff for a most enjoyable and instructive visit and for the very efficient way in which the programme had been carried out.

J. H. Western
Secretary, Plant Pathology Committee

FORAYS

By the Foray Committee

During the period 1897–1939 the Society held sixty-nine major forays devoted to the mycological exploration of localities in the British Isles, namely, five in Scotland, in collaboration with the former Cryptogamic Society of Scotland, four in Ireland, and the remainder in England and Wales. Twenty-seven were spring forays, within the period of 9 May to 10 June, and the remainder autumn forays within the period 5 September to 10 October. On a basis of the collections exhibited on these occasions, supplemented by lists of personal observations supplied by the members present, the Secretary compiled lists of species which were published in the *Transactions*.

There is little doubt that these forays served several useful purposes, as in maintaining a somewhat tenuous 'tradition of species', in introducing members to suitable collecting grounds in districts not personally familiar to them, and, to a rather disappointing extent, in encouraging the study of fungi by local naturalists. The Foray Committee feels, however, that a programme of field work based on a more ecological outlook may be envisaged for the future without losing the advantages of the old forays.

Study of the published lists suggests that the time is ripe to modify the record-taking at forays. For these reasons:

(1) While providing evidence of the occurrence of a fungus in a given district on a given date, the Society's published lists afford little or no clue as to its precise habitat, its relative abundance, or its continuous or discontinuous annual occurrence.

(2) Accurate determination of fungi is notoriously difficult, yet as a rule no indication is afforded of the authority for the published determinations, even of rare or critical species.

(3) No systematic attempt has been made to preserve specimens, or even drawings, of the rarer British species.

The Committee accordingly proposes that:

(1) Each foray should be devoted in part to the collection and examination of the fungus flora of a well-defined type of vegetation. It is hoped in time to cover all the recognized types of woodland and also to visit other types of vegetation, such as moorland, heath, and pasture, each with its characteristic though less abundant fungus flora, which have been much neglected by the Society in the past. It is not proposed to publish separate lists for every foray, but to visit each selected type of vegetation a number of times over a period of years and finally to publish a survey of the fungi found there. With this in view the Committee invites all members present at a foray to co-operate in the more intensive examination of the type of habitat selected, and in the depositing of material of all species collected there in containers provided for the purpose. As has been the practice hitherto, arrangements will be made wherever possible to name and exhibit these collections during the foray. Reports of the year's forays will continue to appear in the *Transactions*, on the lines of those published during the war, but more detailed. They will include observations on collections of special interest and progress reports on the Society's ecological studies.

(2) For the benefit of future workers the referees responsible for the names in published lists should be indicated.

(3) An attempt should be made to preserve representative material of the species recorded and especially of new, rare or critical species, where it will be available for consultation by members or others interested in the validity of a particular record or engaged in monographic study of a species or larger group.

It is hoped in 1946 to revert to the longer spring and autumn forays. The Committee feels, however, that the day forays held at localities easily accessible from London have much to commend them and can be usefully employed to promote a mycological survey of south-eastern England. If this principle is accepted, the longer forays should be devoted to examination of less accessible districts and less-known types of vegetation well outside the London basin.

PROCEEDINGS

Meeting held in the Department of Biology, Chelsea Polytechnic, London, at 11.30 a.m. 17 February 1945. The President, G. Smith, M.Sc., in the Chair.

The dispersal of air-borne fungus spores

P. H. Gregory. Air-borne spore dispersal [see these *Transactions*, xxviii, 26–72].
W. A. R. Dillon-Weston. Observations on spore dispersal.

Discussion to which C. G. Dobbs, C. T. Ingold, E. W. Mason, G. Samuel, and others, contributed.

At the end of the afternoon session the films 'Life Cycle of Pin Mould', 'Potato Blight' and 'Cereal Seed Disinfection' were shown.

Meeting held in the Herbarium of the Royal Botanic Gardens, Kew, at 2.30 p.m. 20 April 1945. The President, G. Smith, M.Sc., in the Chair.

Exhibition of Mycological Books

from the libraries of the Royal Botanic Gardens, Kew, the Imperial Mycological Institute, and Members.

The exhibits, which were commented on by Miss E. M. Wakefield and the Secretary, included illustrated books on the Agaricaceae, nineteenth-century books on plant pathology, the starting-points for international nomenclature, a number of association books, and the Society's collection of local lists.

In addition, there was an exhibit of sclerotia and pseudosclerotia, mostly from the collection of the late Prof. Buller.

CORRECTION

In the paper on 'Some methods for the study of moulds', Fleming and Smith, *Trans. Brit. Myc. Soc.* 1944, xxvii, 13–19, the word 'cellophane' was used inadvertently in such a manner as might create the impression that cellophane is the name of a material. It has been brought to our notice that the word 'Cellophane' is the trade mark of British Cellophane Limited, and denotes exclusively and distinctively the brand of cellulose sheets and films supplied by that Company. The correct designation of the recommended material is regenerated cellulose film, or viscose film.—Ed.

REVIEWS

The Gasteromycetes of Australia and New Zealand. By G. H. CUNNINGHAM. (Dunedin, New Zealand, privately printed, 1944.) Pp. xv + 226. 37 black and white plates, 2 text-figures.

The Gasteromycetes present some difficult problems of both taxonomy and nomenclature. The monographic treatments by De Toni, Ed. Fischer, Hollós and others disagree as to the position to be allotted to certain families and genera, and none has seemed entirely satisfactory. Fischer's classification in the second edition of Engler and Prantl's *Natürliche Pflanzenfamilien* in 1933 differs profoundly from that in the first (1900) edition, particularly in the placing of such genera as *Podaxis* and *Secotium*. Attempts to base classification upon developmental studies have not met with much success, and according to Dr Cunningham 'developmental types have little if any value as a basis for taxonomic treatment of genera and higher ranks'. Most modern workers accept the five orders Phallales, Hymenogastrales, Lycoperdales, Sclerodermales and Nidulariales, which are readily recognized groups, but within them families and genera are not so easily defined. One reason for the confusion existing is undoubtedly the difficulty of obtaining adequate material for study. Apart from the large cosmopolitan genera like *Lycoperdon* and *Geaster*, many of these plants are inhabitants of the desert regions of the globe, and of some species only isolated and poorly preserved specimens have reached European herbaria. Fortunately in recent years mycologists in Australasia, in Africa and America, regions where suitable conditions for the growth of Gasteromycetes are to be found, have turned their attention to the group and there is now a good prospect that a better understanding of these plants will come about.

Dr G. H. Cunningham began work on the Gasteromycetes of Australia and New Zealand more than 20 years ago, and his first revisions appeared in 1924. Since then he has produced a long series of papers, published chiefly in the Proc. Linn. Soc. New South Wales and in the Trans. New Zealand Institute, in which he has dealt successively with all the genera of Gasteromycetes found in the region, and has carried out developmental studies of some species. He has now collected together the results of his research work in the present volume, which is not a mere reprint of the earlier papers but a considered revision of the whole group in the light of knowledge so far attained.

Dr Cunningham's book covers Australia, Tasmania, New Zealand and the contiguous small islands, but not the subtropical islands of Fiji, Samoan Islands, New Hebrides, and New Caledonia. This is to be regretted, for one would have liked to know Dr Cunningham's views on, for instance, the genus *Le Ratia*, described from New Caledonia.

In his introductory matter he discusses among other things the cytology of the Gasteromycetes and studies in development. Following Lohwag and Fischer, four types of development are distinguished, namely lacunar, coralloid, pileate, and multipileate, the latter confined to members of the Clathraceae, and the coralloid to one subfamily of the Hymenogastrales. Since the lacunar and pileate types occur in five and three of the orders respectively, and related genera may show different developmental types, Dr Cunningham comes to the conclusion quoted above as to the taxonomic value of developmental studies. Theories as to phylogeny in the group are at present of little value, but no author seems able to resist making guesses; Dr Cunningham is no exception. There is a summary of the known distribution of genera and species, and a good comparative account of the chief systems of classification which have been proposed, culminating with a key to the arrangement of families and genera adopted by the author. He has the usually accepted five main orders, and follows Fischer's 1900 classification in placing the Secotiaceae as a family in the Hymenogastrales. He rejects entirely the suggestion of Agaric affinities for *Secotium* and *Podaxis*. *Mesophellia*, *Castoreum* and *Abstoma* are put together in the tribe Mesophelliae of Lycoperdaceae. *Phellorina* Berk. and *Chlamydopus* Speg. are classed with *Podaxis* in the subfamily Podaxonoideae of Tulostomaceae. It will be seen from these examples that Cunningham favours Fischer's 1900 classification rather than that adopted in 1933. In this account of classification, the author has italicized the names of certain genera and left others in roman type. In a footnote (p. 31) he says that 'valid genera are given in italics'. Presumably he means 'good' genera, not merely names which are

'valid' nomenclaturally, and one is moved to protest against this all too common confusion in the use of the word 'valid'. Even so, it is difficult to understand quite what the author really intends, for the same name is treated differently on different pages. Thus on p. 34 *Cauloglossum* is italicized, while on p. 35 it is not; *Polyplocium* is italicized on p. 35, and not on p. 36, though on both it is placed in Secotiaceae. The greater part of the volume is occupied by descriptions, with keys to both genera and species. Synonymy is given fully. Certain advances on the author's previous papers are noted at once, as that the genus *Bovistella* Morgan is discarded and the species referred to *Bovista*; similarly the author's genus *Phallobata* (1926) is now referred to *Hysterangium*. Dr Cunningham has followed Miss Morse in the treatment of *Podaxis*, so that he now has only one species instead of two.

In nomenclature he has attempted to follow the International Rules, and has therefore rightly adopted *Geastrum* Pers. instead of *Geaster* Fr. It was not, however, necessary to make 'new combinations' under *Geastrum*, since these two names are orthographic variants; nor did Fischer consider this necessary, although Cunningham cites him as having done so. The nomenclature of fornicate Geasters is extraordinarily difficult, but there seems to be no justification for the adoption of *Geastrum minus* (Pers.) Fischer, using a varietal epithet of Persoon's, since the first epithet used for this fungus in the rank of species was *quadrifidum* Nees (1817), which according to Art. 58 should therefore be adopted. There are a few slips and spelling mistakes which should be corrected if another edition is called for. The author must have a liking for the letter *i*, since almost throughout he spells *Phellorina* Berk. as *Phellorinia*, and *Lycogalopsis* as *Lycogaliopsis*! These small errors do not detract, however, from the great value of the book. It is indispensable to students of the Gasteromycetes of any region. The illustrations are from photographs, and are most valuable when of fresh material. Plates 33–37 are of spores and capillitium, the spores all magnified 700 times, so that they are easily compared.

E. M. Wakefield

Root Disease Fungi. By S. D. Garrett. (Waltham, Mass.: Chronica Botanica Co.; London: Wm. Dawson and Sons, 1944.) 177 pp. 9 figs. $4.50.

Mr Garrett's book is vol. 1 of the *Annales Cryptogamici et Phytopathologici*. It deals in fifteen chapters with a selection of well-known fungi which attack the roots of plants and cause diseases of notable economic importance. The earlier chapters give a general account of the fungi which cause root diseases, with more detailed accounts of those species which the author has chosen for full description; the later chapters deal with the principles of control, mainly in relation to methods of cultivation. Throughout the book, an endeavour is made to emphasize the ecological attitude, and to present fungus, host and environment all as parts of a shifting, living relationship. This is a most welcome attitude, for there can be little doubt that the progress of plant pathology, of mycology, and indeed of botany as a whole, depends much on those practitioners who keep the living organisms in the forefront of their thoughts and work. In intention the book is excellent; regrettably, intention and performance do not match.

The value of Mr Garrett's book is diminished because two separate classes of information have not been kept sufficiently distinct. The presentation lacks in sharpness because the author has been too scrupulous in acknowledging the work of other investigators in a field which he has himself deeply and profitably worked. Acknowledgements, and details of the fungi are so mingled that it is often difficult (and even wearisome) for the reader to get a clear impression either of the fungi or of what has been written about them. The printing of personal names in capital letters, the repetition of the same names in close proximity on the same page, the provision of a long list of references, and then of an index of authors, all these give an impression, no doubt wholly contrary to the intentions of the author, that the book might better have been called *A History of the Investigation of the Root Disease Fungi*; even so, it would have been a chronicle rather than a history.

It is fitting and decent that due acknowledgement should be made when an author uses the work of others. It is common form to make full acknowledgements when a student is preparing a thesis or when an investigator is preparing for publication an account of a detailed piece of work; such writings are provisional in character, and they are not expected to be fully polished. In contrast, a book should have a finished appearance;

it should set out clearly what the author knows and thinks about his chosen subject, and it should not lay on to the reader the task of sorting out for himself the diverse lines of knowledge covered by the book. Mr Garrett's wish to give full recognition to his sources has hindered him from helping his readers as fully as could be desired.

Root Disease Fungi will be a useful source of information to the specialist, but it will not be the everyday companion of the general student. In due time, doubtless, it will engender a more mature and polished account of an interesting and important set of fungi. The knowledge which Mr Garrett has spread out shows that an intelligent use of biological methods of control may well lead to better results than have been obtained by some of the rough and ready methods of the past.

The book is well printed and bound, but the price is rather high for a book containing so few illustrations; that high price is no doubt due to the war.

B. Barnes

An Introduction to the Taxonomy and Nomenclature of Fungi. By G. R. Bisby. (Imperial Mycological Institute, Kew, Surrey, 1945.) 117 pp. 5*s*.

The lack of interest, and even impatience, often shown by naturalists when a discussion arises on the principles of taxonomy and nomenclature is regrettable, but too often those principles are discussed in an atmosphere of mystery which is repellent to workers whose primary interest is in living things. The title of Dr Bisby's book may well mislead, for that title, while fairly indicating the subject of the book, gives no hint of the broad common sense and ripe experience which show on every page that the author has written. Dr Bisby has put into print the things that many of us have said when we have been trying to encourage the young idea, but no one seems before to have included between the covers of one book all that the author has now set down, nor to have given sound guidance in so attractive a form; it is remarkable how dry bones have been made alive. Dr Bisby does not try to play at the now somewhat discredited diversion of debunking, but a reader who knows him can sense the undercurrent of kindly fun, and as he reads can picture the author writing many a sentence with more than a twinkle in his eye.

While it may be that the younger workers in mycology will benefit most from this book, there is much in it that should be of value to the practising botanist, no matter what his special interests may be.

The last fifty pages of the book are occupied by a reprint of the current version of the International Rules of Botanical Nomenclature. These Rules have not been so generally available as could be wished, so that the reprint satisfies a real need. To the reprint, Dr Bisby has added a number of comments and suggestions which provoke thought and may stimulate some necessary action.

B. Barnes

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Bruxelles, Jardin Botanique de l'État, c/o M. P. van Aerdschot. (1911.)
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Fletcher, Mrs P. T., B.A., 11 Arundel Court, Jubilee Place, Chelsea, London, S.W. 3. (1935.)
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Gardner, Capt. Frederic, c/o Barclays Bank, Jersey, C.I. (1898.)
Garrett, S. D., M.A., D.I.C., Rothamsted Experimental Station, Harpenden, Herts. (1936.)
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Gilbert, E. J., Docteur en Pharmacie, 4 Rue de Musset, Paris (16e), France. (1924.)
Gilbert, Dr E. M., Botanical Department, University of Wisconsin, Madison, Wis., U.S.A. (1922.)
Gill, G. E., LL.B., Law Library, Four Courts, Dublin. (1937.)
Gillespie, J., B.Sc., Department of Botany, The University, Reading. (1938.)
Gilson, Mrs M. R. [née Brown], Newnham College, Cambridge. (1936.)
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Goodman, R. E. J., Norfolk Flax Establishment, Flitcham Abbey, Flitcham, King's Lynn, Norfolk. (1944.)
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Graddon, W. D., The Brooms, Park Lane, Congleton, Cheshire.
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Grainger, J., B.Sc., Ph.D., Department of Plant Pathology, West of Scotland Agricultural College, Auchincruive by Ayr. (1944.)
Gray, Miss E. G., B.Sc., Ph.D., North of Scotland Agricultural College, 41½ Union Street, Aberdeen. (1942.)
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Hull, R., B.Sc., Ph.D., A.R.C.S., Midland Agricultural College, Sutton Bonington, Loughborough. (1942.)
Hull, The Librarian, Botanical Department, University College. (1929.)
Humphrey, Dr C. J., 543 No. La Cienega Blvd., Los Angeles, Calif., U.S.A. (1921.)
Hurst, C. P., F.L.S., Landulph Rectory, Saltash, Cornwall. (1928.)
Ingold, Professor C. T., D.Sc., Ph.D., F.L.S., Department of Botany, Birkbeck College, Chancery Lane, London, E.C. 4. (1935.)
Iowa, The Library, State University of Iowa, Library Annex, Iowa City, U.S.A. (1923.)
Iowa State College, Library, Ames, Iowa, U.S.A. (1927.)
Isaac, I., B.Sc., East Malling Research Station, nr. Maidstone, Kent. (1943.)
Issatchenko, Professor Dr B. L., Nowinskii B. 25, log. 11, Moscow 69, U.S.S.R. (1923.)
Jenkins, Miss Anna E., Bureau of Plant Industry, Department of Agriculture, Washington, D.C., U.S.A. (1942.)
John Crerar Library, 86 East Randolph Street, Chicago, Illinois, U.S.A. (1929.)
Johnstone, R. H., 726 Anniesland Road, Glasgow, W. 4. (1938.)
Jones, G. H., M.A., Kasenga, Stanley Avenue, Chesham, Bucks. (1922.)
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Keay, Miss M. A., M.A., Ph.D., Norfolk Flax Establishment, Flitcham Abbey, Flitcham, King's Lynn, Norfolk. (1935.)
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Knight, Major Maxwell, O.B.E., The Homestead, Park Road, Camberley, Surrey. (1945.)
Knight, Mrs S., The Homestead, Park Road, Camberley, Surrey. (1945.)
Kuala Lumpur, F.M.S., The Director of Agriculture, Straits Settlements and Federated Malay States. (1930.)

Layton, T. A., 1 Keppel Street, London, W.C. 1. (1945.)
Leach, R., B.A., Department of Agriculture, Kingston, Jamaica. (1929.)
Legge, Miss B. J., Pinetrees, The Wergs, Wolverhampton. (1943.)
Leicester, The City Museum. (1923.)
Levisohn, Miss I., D.Phil., Forestry School, 6 Keble Road, Oxford. (1943.)
Linder, Dr D., Farlow Herbarium, Harvard University, 20 Divinity Avenue, Cambridge, Mass., U.S.A. (1935.)
Line, James, M.A., School of Agriculture, Cambridge. (1921.)
Linnean Society, The, Burlington House, Piccadilly, London, W. 1. (1919.)
Lloyd Library, The, 309 West Court Street, Cincinnati, 2, Ohio, U.S.A. (1907.)
Loader, Miss F. M., B.Sc., Botanical Department, University College, Southampton. (1927.)
Long, Mrs E. M. [née Ellis], B.A., B.Sc., 26 Constitution Hill, Norwich. (1930.)
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Lütjeharms, Professor W. J., Phil.Nat.D., Department of Botany, University College, Bloemfontein, Orange Free State, S. Africa. (1930.)
Macdonald, James A., Botany Department, The University, St. Andrews. (1938.)
McKay, Robert, B.Sc., A.R.C.S.I., Department of Plant Pathology, Albert Agricultural College, Glasnevin, Dublin. (1939.)
McQuillan, Miss C. M., Skipton Girls' High School, Skipton, Yorks. (1944.)
Marsh, R. W., M.A., Research Station, Long Ashton, Bristol. (1923.)
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Matthews, Professor J. R., M.A., F.L.S., Department of Botany, The University, Old Aberdeen. (1921.)
Mehta, Professor K. C., Ph.D., Department of Biology, Agra College, Agra, U.P., India. (1921.)
Metcalfe, C. R., B.A., Ph.D., Jodrell Laboratory, Royal Botanic Gardens, Kew, Surrey. (1926.)
Michigan Agricultural College Library, East Lansing, Michigan, U.S.A. (1924.)
Miller, Professor J. H., B.S., M.S., Ph.D., University of Georgia, Athens, Ga., U.S.A. (1930.)
Millidge, P. H., 205 Carisbrooke Road, Newport, I.O.W. (1937.)
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Moore, Miss F. J., Ph.D., Rothamsted Experimental Station, Harpenden, Herts. (1945.)
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Moore, W. C., M.A., Ministry of Agriculture, Plant Pathology Laboratory, Milton Road, Harpenden, Herts. (1922.)
Morris, L. E., c/o Eton College, Windsor, Berks. (1924.)
Moureau, J., Laboratoire de Phytopathologie, I.N.E.A.C., Bambesa, Belgian Congo. (1944.)
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Munro, Miss M. C. D., Ph.D., 12 Blantyre Terrace, Edinburgh, 10. (1945.)
Munson, R. G., 10 Abbotsbury Gardens, Eastcote, Pinner, Middlesex. (1943.)
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National Collection of Type Cultures, Curator, Lister Institute, Elstree, Herts. (1921.)
National Museum of Wales, Cardiff. (1924.)
Nattrass, R. M., B.Sc. (Agric.), Ph.D., Department of Agriculture, P.O.B. 338, Nairobi, Kenya. (1925.)
Nederlandsche Mycologische Vereeniging, The Librarian, Zoornweg 10, Wageningen, Holland. (1920.)
Newcastle-on-Tyne, The Librarian, King's College. (1928.)
New York Botanical Garden, Bronx Park, New York, U.S.A. (1904.)
Nierenstein, M., D.Sc., 2 Rylestone Grove, Bristol, 9. (1945.)
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North Carolina, Library, University of, Chapel Hill, North Carolina, U.S.A. (1920.)
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Nursery and Market Garden Industries' Development Society, Ltd., Experimental and Research Station, Cheshunt, Herts. (1922.)
O'Connor, P., Ph.D., B.Sc., A.R.C.Sc.I., National Museum, Dublin. (1925.)
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Ontario Agricultural College, Library, Guelph, Ontario, Canada. (1920.)
Osborn, Professor T. G. B., D.Sc., F.L.S., Department of Botany, The University, Oxford. (1910.)
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Pettifer, A. J., 36 Cheviot Gardens, Hendon Way, London, N.W. 2. (1944.)
Peyronel, Dr Benjamino, R. Istituto Sup. Agrario e Forestale, Piazzale del Re, Firenze, Italy. (1932.)
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Pineapple Research Institute, The Library, P.O. Box 3166, Honolulu, Hawaii. (1920.)
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Pretoria, South Africa, The Librarian, Division of Botany and Plant Pathology, P.O. Box 994. (1922.)
Ramsbottom, J., O.B.E., Dr.Sc., M.A., F.L.S., British Museum (Nat. Hist.), Cromwell Road, South Kensington, London, S.W. 7. (1910.)
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Rose, H. V., Morden College, Blackheath, London, S.E. 3. (1944.)
Rothamsted Experimental Station, Department of Plant Pathology, Harpenden, Herts. (1923.)
Rothwell, M. S., Africa House, Kingsway, London, W.C. 2. (1945.)
de Rousset-Hall, O., B.A., Low Temperature Research Station, Cambridge. (1942.)
Royal Holloway College, Englefield Green, Surrey. (1942.)
Rutgers College and State University of New Jersey, Library, New Brunswick, New Jersey, U.S.A. (1922.)
St Paul, Minnesota, U.S.A., The Library, Department of Agriculture, University Farm. (1920.)
Sampson, Miss K., M.Sc., Malmsmead, Lacey Green, nr. Aylesbury, Bucks. (1920.)
Samuel, Geoffrey, M.Sc., Ministry of Agriculture, Plant Pathology Laboratory, Milton Road, Harpenden, Herts. (1923.)
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Searle, G. Odell, B.Sc. (Agric.), Flax Research Institute, Flitcham Abbey, Flitcham, King's Lynn, Norfolk. (1920.)
Seth, N. L., B.Sc., Ph.D., D.I.C., Agricultural College, Mandalay, Burma. (1930.)
Shear, Dr C. L., U.S. Department of Agriculture, Bureau of Plant Industry, Washington, D.C., U.S.A. (1930.)
Sheard, Mrs E., Experimental and Research Station, Cheshunt, Herts. (1937.)
Skene, Professor Macgregor, Department of Botany, The University, Bristol. (1936.)
Smith, Alexander, M.A., Ph.D., Ministry of Agriculture, Plant Pathology Laboratory, Milton Road, Harpenden, Herts. (1924.)
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Smith, Miss K. Goldie, 12 Victoria Park Road, Leicester. (1944.)
Smith, Professor Noel J. G., Ph.D., B.Sc., Botany Department, Rhodes University College, Grahamstown, S. Africa. (1924.)
South London Botanical Institute, 323 Norwood Road, Tulse Hill, London, S.E. 24. (1921.)
Sowter, F. A., F.L.S., 9 North Avenue, Leicester. (1942.)
Stakman, Professor E. C., University of Minnesota, Department of Agriculture, University Farm, St Paul, Minn., U.S.A. (1922.)

Stationery Office, H.M., Superintendent of Publications, Book Dept., Westminster, S.W. 1. (5 subscriptions.) (1920.)
Stephens, Miss E. L., B.A., Department of Botany, University of Cape Town, South Africa. (1928.)
Sterry, Miss M., B.Sc., Manor Cottage, Longhope, Glos. (1942.)
Stevenson, Dr J. A., U.S. Department of Agriculture, Bureau of Plant Industry, Washington, D.C., U.S.A. (1927.)
Stewart, Miss S. B., Insects Pests Laboratory, 30 High Street, Steyning, Sussex. (1944.)
Steyaert, R. L., Ing. A.I.Gx., Laboratoire Bambesa, Uele, Belgian Congo. (1931.)
Stiles, Professor W., Sc.D., F.R.S., Botanical Department, The University, Edgbaston, Birmingham, 15. (1936.)
Stirrup, H. H., M.Sc., Midland Agricultural College, Sutton Bonington, Loughborough. (1922.)
Storey, H. H., M.A., Ph.D., East African Agricultural Research Institute, Amani, Tanganyika Territory, East Africa. (1922.)
Storey, I. F., Ph.D., Department of Agriculture, The University, Leeds, 2. (1941.)
Swanton, E. W., M.B.E., A.L.S., Educational Museum, Haslemere, Surrey. (1899.)
Swedish Academy of Sciences, Royal, Stockholm, Sweden. (1919.)
Sydney, Australia, The Librarian, University of. (1922.)
Tennessee, University of, Agricultural Experiment Station, Library, Knoxville, Tennessee, U.S.A. (1926.)
Tervet, I. W., B.Sc., Department of Plant Pathology, University Farm, St Paul, Minn., U.S.A. (1933.)
Thirumalachar, M. J., M.Sc., D.Sc., 20th V Main Road, Malleswaram, Bangalore, India. (1945.)
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Thompson, Miss M. V., Pathological Research Laboratory, Christie Hospital and Holt Radium Institute, Manchester, 20. (1942.)
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Tomkins, R. G., M.A., Ph.D., Trinity College, Cambridge. (1925.)
Tunstall, A. C., Tocklai Experimental Station, Cinnamara P.O., Assam, British India. (1933.)
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Vanterpool, T. C., M.Sc., Botanical Department, University of Saskatchewan, Saskatoon, Canada. (1929.)
Venkatarayan, S. V., Mycologist, Agricultural Department, Bangalore, S. India. (1935.)
Wadham, Professor S. M., M.A., Department of Agriculture, The University, Melbourne, Victoria, Australia. (1922.)
Waldie, J. S. L., B.Sc., C.D.A., Department of Agricultural Botany, The University, Reading. (1925.)
Wales, University College of, Librarian, Botanical Department, Aberystwyth, North Wales. (1927.)
Wallace, E. R., Agricultural Institute, Kirton, nr. Boston, Lincs. (1934.)
Wallace, G. B., B.Sc. (Agric.), Ph.D., Lyamungu, Moshi, Tanganyika Territory, E. Africa. (1928.)
Wardlaw, Professor C. W., Department of Cryptogamic Botany, The University, Manchester, 13. (1943.)

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Washington, State College of, Pullman, Wash., U.S.A. (1924.)
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Whitaker, F. Owen, 51 Grosvenor Avenue, Carshalton, Surrey. (1921.)
White, Neville, Tasmanian Department of Agriculture, Box 673E, G.P.O., Hobart, Tasmania. (1944.)
Whitehead, T., D.Sc., A.R.C.S., University College of North Wales, Bangor. (1920.)
Wilkins, W. H., M.A., D.Phil., Department of Botany, The University, Oxford. (1928.)
Wilkinson, E. H., Research Station, Long Ashton, Bristol. (1938.)
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Wilson, Malcolm, D.Sc., A.R.C.S., F.L.S., Royal Botanic Garden, Edinburgh. (1912.)
Wiltshire, S. P., D.Sc., Imperial Mycological Institute, Ferry Lane, Kew, Surrey. (1920.)
Wisconsin, The Library, University of, Madison, Wis., U.S.A. (1923.)
Wolf, Dr F. A., Department of Botany, Duke University, Durham, North Carolina, U.S.A. (1940.)
Wolf, Dr F. T., Vanderbilt University, Nashville, Tennessee, U.S.A. (1940.)
Wood, F. C., The Rest, Franklin Road, Durrington, Worthing. (1935.)
Woodcock, A. J. A., M.Sc., F.E.S., Rhianva, 65 Rock Avenue, Gillingham, Kent. (1926.)
Woodward, R. C., Ph.D., Hawthorndale Laboratories, Jealott's Hill Research Station, Bracknell, Berks. (1924.)
Woolhope, The Naturalists' Field Club, Hereford. (1896.)
Wormald, H., D.Sc., A.R.S.C., East Malling Research Station, nr. Maidstone, Kent. (1921.)
Yale University, Library, New Haven, Connecticut, U.S.A. (1930.)
Yuill, E., Norwood, Towthorpe Lane, Haxby, York. (1937.)
Zürich, Switzerland, Botanical Garden and Museum, c/o Dr A. U. Däniker. (1921.)
Zürich, Institut für Spezielle Botanik der Eidg. Techn. Hochschule. (1928.)

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